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**ANIMAL LIFE**  
**AN EVOLUTIONARY NATURAL HISTORY**

GENERAL EDITOR: W. P. PYCRAFT  
ZOOLOGICAL DEPARTMENT, BRITISH MUSEUM

**REPTILES, AMPHIBIA, FISHES, AND  
LOWER CHORDATA**

EDITED BY  
**J. T. CUNNINGHAM, M.A. OXON.**

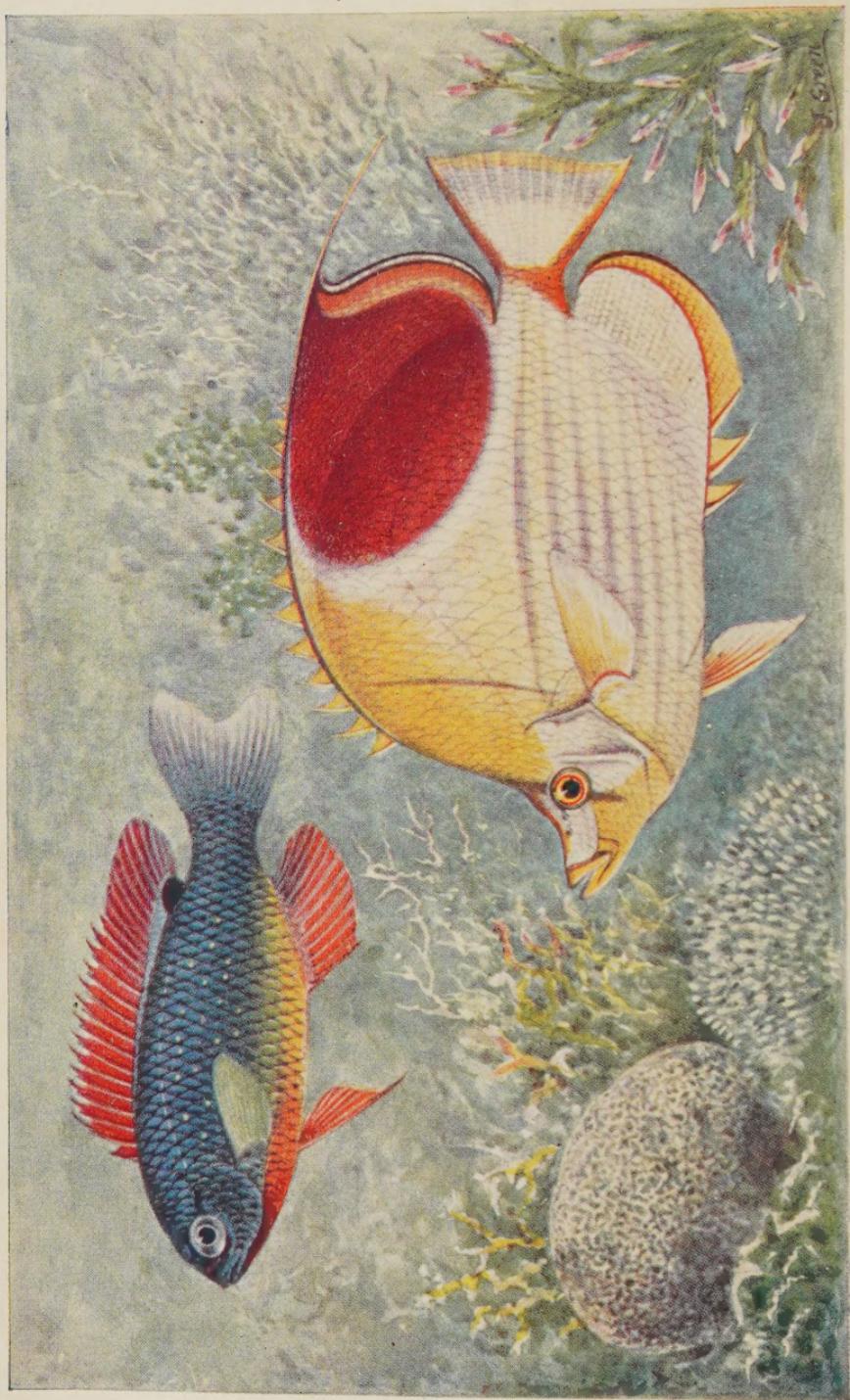
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A SPECIMEN OF THE POMACENTRIDAE AND ONE OF THE CHAETODONTIDAE, ILLUSTRATING THE BRILLIANT COLORATION OF THESE TROPICAL FAMILIES OF FISHES. A.—*ABUDEFDUF TAUPON*, SAMOA. (POMACENTRIDAE). B.—*TETRAGONOPTERUS EPHIPPUM*, EAST INDIES. (CHAETODONTIDAE).

# REPTILES AMPHIBIA FISHES AND LOWER CHORDATA

BY

RICHARD LYDEKKER

J. T. CUNNINGHAM, M.A. OXON.

G. A. BOULENGER, D.Sc., F.R.S.

AND

J. ARTHUR THOMSON, M.A.

WITH FOUR PLATES IN COLOUR, THIRTY-THREE IN MONOTONE, A MAP,  
AND MANY TEXT FIGURES

577.

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## PREFACE

THE kindly reception accorded to "A History of Birds"—the second in the order of final sequence of this series—encourages me to believe that these volumes on vertebrate animal life which I projected really supplied a need felt by that increasing body of men and women who profess themselves "nature lovers".

Having conceived the plan of recording, at any rate in broad outline, the history of the vertebrates from the evolutionist's point of view, I allotted to myself, as many already know, the task of writing the volume on Birds, and proposed to edit the remaining volumes rather than attempt to write them. And this because the day is now past when any single writer can hope to achieve such a task with even tolerable success, for this is the day of specialists. As a consequence, for the first time in the annals of natural history, the complete life-story of the reptiles, amphibia, and fishes, and those primitive creatures which lie at the foundations, so to speak, of the great house of the vertebrates, is told as only specialists can tell it. The very existence of these primitive animals is unsuspected by most of us, but, as Professor Arthur Thomson shows, they present us with some most interesting and most important problems. The student of sociology will find in his chapters, no less than in those concerning more familiar creatures, much food for reflection bearing on the subjects of adaptation to environment, degeneration, and so on.

Those who seek to discover the subtle and mysterious factors which govern the transformation of animals will find much food for thought in Mr. Lydekker's account of the reptiles, and in the chapters on the nursing habits of amphibia and fishes by Mr. G. A. Boulenger and Mr. J. T. Cunningham; and to these we would add the weird and fascinating chapter on the fish-life of the abysses of the ocean—a world wherein the light of day never penetrates, and where the pall of night is broken only by the pale phosphorescence emitted by the creatures doomed to dwell there!

The names of the contributors to this volume alone vouch for the sterling merit of its contents: for they are men of established reputation. It is, therefore, unnecessary to say anything of their attainments. But I should like to thank them here for the help they have so generously given me in my endeavour to make these volumes a landmark in the annals of zoological literature. Some of our neighbours assure us that "Darwinism is dead". If these pages show anything they show that the contrary is emphatically the case!

Though my task as Editor, with such contributors, could not but be an easy one as to the substance of the work, yet the burden imposed by purely mechanical details was really heavy, so much so that ill-health compelled me to hand over my labours before they had well begun to my friend, Mr. J. T. Cunningham. He has, however, displayed such scrupulous care and zeal that my practical retirement has in no way injured the scheme I had so much at heart.

W. P. PYCRAFT

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## SECTION I

# REPTILES

### CHAPTER I

#### GENERAL CHARACTERS

Reptiles in general. Definition of reptiles. Variety of forms. Extremes of size. Some leading structural features of the class.

OUR forefathers of classic days evidently had no acquaintance with either the flying pterodactyles, the bipedal iguanodons, or the whale-like ichthyosaurs of a long past epoch, or, for the matter of that, with the so-called flying dragons of the Malay countries of to-day. Otherwise they would scarcely have applied the name reptiles (Latin *repo*, Greek *ἔρπω*) to the creatures forming the subject of the present section, together with frogs, salamanders, and their kin, which constitute the class Amphibia, or Batrachia. As a matter of fact, however, having eliminated the Amphibia, and regarding the marine turtles as forming the exception which proves the rule, we find that, etymologically, the term reptiles adequately expresses one of the leading external features of the existing members of the class. For modern reptiles, whether provided with limbs or no, are essentially creatures whose "belly cleaveth to the ground," and which consequently creep (or "reep") in the true sense of the word. Indeed, the one great external characteristic of nearly all limbed reptiles of to-day is that the body is carried close to or even touching the ground, and is never raised high above it in the manner characteristic of mammals and the majority of birds. In some of the arboreal forms this trait is less marked, while

species like the Australian frilled lizard, which at times run on their hind legs, form in some degree an exception ; but in the main the diagnosis is true.

Seeking for something more nearly approaching a scientific definition, and confining our attention to the living members of the class, it may be affirmed that reptiles are cold-blooded vertebrates, unprovided with hair or feathers, which breathe atmospheric air by means of lungs, and do not undergo a marked transformation, or metamorphosis, after leaving the egg, whereby they pass from gill-breathing to lung-breathing creatures. By the first two characters they are distinguished from mammals and birds ; by the third, coupled with the circumstance that their limbs do not partake of the character of fins, they are differentiated from fishes ; while in the fourth feature they differ from amphibians in general, despite the fact that certain more specialised members of the latter have "slipped" some or all of the early stages of development.

Another important feature of modern reptiles, and one also available in the case of their fossil relatives, is that the skull is articulated to the first vertebra by means of a single, although tripartite, knob, known as the occipital condyle ; this character distinguishing them from mammals and amphibians, although not from birds.

When we endeavour to go much further in regard to differentiating both recent and fossil reptiles from the other three classes of terrestrial vertebrates, we shall be met with increasing difficulties. For it is manifest that while reptiles are descended from amphibians, it is equally clear that reptiles themselves have given origin on the one hand to birds and on the other to mammals. Consequently, were the whole scheme of animated nature displayed before our eyes, we should expect to find amphibians with a single occipital condyle formed by the development of a median element between the two lateral ones, and without a metamorphosis or, what is the same thing, reptiles with a metamorphosis. On the other hand, we should look for reptile-like creatures approximating more or less closely to birds, and acquiring at some stage of their development wings of a bird-like type, feathers, and warm blood. Indeed, for all we know, pterodactyles, although off the bird-line, may have been (and very probably were) warm-blooded.

Finally, there must have been mammal-like reptiles which acquired two occipital condyles by the suppression of the median element of the reptilian one, and at some stage of their progressive evolution exchanged their scales (if they possessed them) for hair, and likewise raised the temperature of their blood markedly above that of the surrounding medium.

Obviously, then, as in all analogous instances, it is not of much use attempting to define distinctions which may have never existed between extinct reptiles and the other three classes of terrestrial vertebrates. It must therefore suffice to give the foregoing definition of existing reptiles, and to consider that such extinct vertebrates as come within its limits, or which approximate more or less closely thereto, are likewise to be included within the limits of the class.

Existing reptiles include only a small number of leading groups, or orders; but such groups do not altogether coincide with the popular classification of these creatures. In popular language reptiles are roughly classed as crocodiles (inclusive of alligators and gharials), tortoises and turtles, lizards, and snakes. Crocodiles, in this wider sense, constitute an ordinal group (*Crocodilia*) by themselves, as do tortoises and turtles a second (*Chelonia*). Here, however, the agreement between popular and scientific classification ceases, for whereas in the former the lizard-like tuatera (*Sphenodon*) of New Zealand is reckoned as a lizard, in the latter it is regarded as the sole surviving representative of an extremely generalised order (*Rhynchocephalia*), with but little in common with the group in which the true lizards are included. Again, lizards and snakes are popularly classed as widely sundered groups, whereas in the scientific scheme the two (exclusive of the aforesaid tuatera) are brigaded in a single group (*Squamata*) ranking in value with the *Crocodilia*, *Chelonia*, and *Rhynchocephalia*. Nor is this all, for chamaeleons, which are commonly regarded as lizards, are considered by some naturalists to form a third subgroup (*Rhiptoglossa*) of the *Squamata*, with the same value as the two respectively containing the lizards (*Lacertilia*) and the snakes (*Ophidia*). Recent reptiles and their immediate extinct kindred are consequently classed as follows:—

## REPTILES

Order I. Rhynchocephalia—Tuatera.

II. Crocodilia—Crocodiles, alligators, etc.

III. Chelonia—Tortoises and turtles.

IV. Squamata.

Suborder I. Rhiptoglossa—Chamæleons.

2. Lacertilia—Lizards.

3. Ophidia—Snakes.

When, however, extinct types are also taken into consideration, the list becomes greatly extended, and we have the following orders of leading groups, viz. :—

Subclass I. Theromorpha—Mammal-like brigade.

Order I. Pariasauria.

II. Cotylosauria.

III. Anomodontia.

Subclass II. Ornithomorpha—Bird-like brigade.

Order IV. Rhynchocephalia—Tuateras.

V. Pelycosauria.

VI. Parasuchia—Belodonts.

VII. Acrosauria.

VIII. Squamata—Lizards and snakes.

Suborder I. Rhiptoglossa—Chamæleons.

2. Lacertilia—Lizards.

3. Pythonomorpha — Sea-serpents.

4. Dolichosauria — Snake-lizards.

5. Ophidia—Snakes.

IX. Chelonia—Tortoises and turtles.

X. Placodontia—Bean-toothed reptiles.

XI. Sauropterygia—Plesiosaurs.

XII. Ichthyopterygia—Ichthyosaurs.

XIII. Crocodilia—Crocodiles.

XIV. Dinosauria—Giant reptiles.

XV. Ornithosauria—Pterodactyles.

It should be mentioned that a somewhat different arrangement of the two main divisions of reptiles has been proposed ; some authorities including within the first brigade (under the name of Synapsida) the Chelonia and Sauropterygia, on the ground that they agree with the Theromorpha in possessing single or united temporal arches, and including in the second

brigade, under the name of Diapsida, all the other orders, which are characterised primarily by the possession of double or separated temporal arches.<sup>1</sup> It has been pointed out, however, that it is illogical to separate widely from one another groups like the Chelonia, Sauropterygia, Rhynchocephalia, and Crocodilia, all of which agree in the possession of abdominal ribs (modified in the first into a true plastron); and, moreover, that the Theromorpha differ much more widely from all other groups of reptiles collectively than do any of the latter from one another.

An alternative classification, in which some of the groups ranked above as orders are reduced to the grade of suborders, is the following:—

Extinct Groups are marked with a †

	ORDER	SUBORDER
Mammal-like Brigade	I. + ANOMODONTIA Anomodonts	{ 1 Dicynodontia 2 Theriodontia 3 Crotosaura 4 Pariasaura
Bird-like Brigade	II. RHYNCHOCEPHALIA Tuateras	{ 1 † Protorosauria 2 Rhynchocephalia Vera 3 Acrosaura
	III. + PELOCOSAURIA	
	IV. SQUAMATA Snakes and Lizards	{ 1 Lacertilia 2 Rhiptoglossa 3 Ophidia 4 † Dolichosauria 5 † Pythonomorpha
	V. CHELONIA Tortoises and Turtles	{ 1 Cryptodira 2 Pleurodira 3 † Amphichelydia 4 Trionychoidia
	VI. PLACODONTIA Placodus	
	VII. + SAUROPTERYGIA Plesiosaurs	
	VIII. + ICHTHYOPTERYGIA Ichthyosaurs	
	IX. CROCODILIA Crocodiles	{ 1 Eusuchia 2 † Aëtosauria 3 † Parasuchia
	X. + DINOSAURIA Dinosaurs	{ 1 Theropoda 2 Sauropoda 3 Ornithopoda
	XI. + ORNITHOSAURIA Pterodactyles	

The length of the foregoing lists, as compared with the one dealing solely with existing forms, must very materially modify

<sup>1</sup> In the Squamata the lower temporal arch has disappeared.

our conception of the relative importance of the class Reptilia in the animal kingdom; showing, as it does, that in place of comparatively few, the class really contains a very large number of widely different structural types. A mere inspection of the lists does not, however, by any means reveal all that is implied as regards the differences between recent and extinct reptiles. For example, with the exception of crocodiles and their kin, giant land-tortoises and turtles, and pythons and anacondas, no modern reptiles can be regarded as really large animals, while the great majority of the class are comparatively small creatures. Even in the case of crocodiles and alligators a length of twenty-five feet is but very rarely, if ever, attained; while thirty feet is an unusually large size for a python or an anaconda, although it is possible that individuals considerably exceeding these dimensions may now and then be met with. Again, as already stated, practically all the recent members of the class are characterised by the relative shortness of their limbs (when these appendages are present at all), and the consequent approximation of the lower surface of the body to the ground.

Contrast the comparatively small dimensions and creeping gait of the majority of living types of reptiles with the huge bulk and the elevated or even upright position of the body in many of their extinct relatives of the Jurassic and Cretaceous epochs. The American dinosaur *Diplodocus*, for instance, had an approximate length of between sixty and seventy feet, and probably stood not far short of twelve or thirteen feet in height; while its relative the iguanodon, when in its habitual upright position, towered to something like twenty feet. The body, too, of *Diplodocus* and its four-footed relatives was raised so much above the ground that a man somewhat below the ordinary stature could have probably walked under its belly without much stooping.<sup>1</sup> During the same epochs the seas were inhabited by gigantic ichthyosaurs and plesiosaurs, which filled the place in nature now occupied by whales, and some of the larger and more typical representatives of which attained dimensions of between thirty and forty feet, or possibly even more. Larger still were those big-headed members of the plesiosaurian group known as pliosaurs, in which the length of

<sup>1</sup> Some naturalists are of opinion that *Diplodocus* had a pose like that of a crocodile, with the belly close to the ground.

the lower jaw was close on six feet and that of the thigh-bone, or femur, fully a yard, from which some estimate may be formed as to the total dimensions of these monsters. As the plesiosaurs and ichthyosaurs began to wane, their place was filled by the sea-serpents, or Pythonomorpha, of the Upper Cretaceous, the length of some of which is estimated at not less than forty feet. Neither were these huge bodily dimensions by any means confined to the extinct Mesozoic ordinal groups, for we find many of the Lower Eocene, and even in some cases the later Tertiary, representatives of modern groups far exceeding in point of size their living relatives. The giant *Eochelone* of the London Clay had, for instance, a skull fully three times the size of that of the modern leathery turtle, or luth (*Dermochelys*) which is itself one of the largest of living reptiles; while a snake (*Gigantophis*) from the Lower Eocene of Egypt probably fell but little short of fifty feet in length. Again, in the Lower Pliocene the gharial-like *Rhamphosuchus* of India has been estimated to have reached a length of between fifty and sixty feet; while in the Pleistocene the giant monitor (*Varanus priscus*) of Queensland probably grew to something like fifty feet.

Finally, as the dinosaurs or giant land-reptiles, and the earlier mammal-like theromorphs took the place during the Mesozoic epoch now held by terrestrial mammals, while the ichthyosaurs, plesiosaurs, and sea-serpents played the part of the whales of our modern seas, so the flying pterodactyles fulfilled the rôle of birds, which during the earlier part of that era of the world's evolution were probably non-existent, while in the later stages of the same they apparently occupied a subordinate position and had not yet gained the dominion of the air. As the crocodiles, tuateras, and tortoises and turtles of the Mesozoic represented the reptiles of the present day, it is thus evident that the reptilian class, at that distant epoch, occupied the positions in nature now filled collectively by mammals, birds, and reptiles, and that the title "age of reptiles" which has been bestowed on the era in question is fully justified.

"It is noteworthy," writes Dr. A. Smith Woodward, "that nearly all reptiles with well-formed limbs—whether adapted for habitual support of the body on land, for flight, or for constant swimming—flourished only before mammals and birds became dominant; the vast majority of the survivors during

the Tertiary period and in the existing world being comparatively degenerate types."

A few of the distinctive features of the reptilian class have been already mentioned ; these and others may now be somewhat more fully noticed, especially when they display marked adaptive or evolutionary modifications. First, with regard to the single occipital condyle by means of which the skull is articulated to the atlas, or first, vertebra in all existing reptiles and probably also in all extinct ones with the possible exception of some of the anomodonts. In its most typical form, as exemplified by crocodiles and alligators, this condyle consists of a single knob formed exclusively by the basioccipital bone of the skull ; it is then known as the typical monocondylic form. In many reptiles, such as iguanas, pythons, and turtles, lateral elements are developed to a larger or smaller extent from the exoccipital bones, and the structure then becomes of the tripartite monocondylic type. In some tortoises (*Testudo*), and more especially in the anomodonts (such as *Dicynodon* and *Cynognathus*) the lateral elements tend to develop at the expense of the median basioccipital element, which becomes greatly reduced, and we thus have the transitional dicondylic type, which, it is noteworthy, also exists in certain mammals. Finally, the total disappearance of the basioccipital element would result in the typical dicondylic form, or, in other words, in the double condyles of ordinary mammals. Such (to somewhat anticipate matters) appears to have been the mode in which the double occipital condyles of mammals have been evolved from the single reptilian condyle. Here it may be mentioned that amphibians also possess double condyles, and it was accordingly at one time supposed that mammals took their origin from amphibians rather than from reptiles, but there are structural features which militate strongly against such a view. The single monocondylic type has, on the other hand, persisted in the evolution of reptiles to give origin to birds.

The next most important feature in the skeleton of reptiles is the fact that, as in birds, the mandible, or lower jaw, consists of a number of separate bony elements, and articulates with the squamosal region of the cranium, or skull proper, by means of a quadrate bone. Much discussion has taken place as regards the fate of the quadrate bone when the theromorph reptiles

developed into mammals, in which the mandible articulates directly with the squamosal, and consists of only a single element on each side, corresponding to the dentary bone in the reptilian lower jaw. According to one of the latest authorities<sup>1</sup> on this intricate subject, it seems probable that the reptilian quadrate has been taken up into the internal ear of mammals to form the incus, while the articular, or hindmost bone, of the lower jaw of the former has likewise been incorporated in the same region of the ear, where it forms the malleus. It is added that a meniscus of cartilage found between the condyle of the lower jaw and the squamosal in most mammals is a new element, unrepresented in reptiles.

Another interpretation of the fate of the quadrate is, however, suggested by Dr. R. Broom,<sup>2</sup> who has paid particular attention to the relationship existing between the theriodont anomodonts and mammals. After pointing out that, according to his interpretation, the quadrate in the theriodonts is reduced to an exceedingly small bone affixed to the extremity of the squamosal, the author suggests that the reptilian quadrate is represented by the aforesaid meniscus, or interarticular cartilage, in mammals. "On the other hand," he adds, "it is quite possible that the quadrate is entirely absent in all mammals; yet the presence of a cartilaginous element in a situation exactly corresponding to that of the quadrate in theriodonts seems strongly to favour the view that in the meniscus we have the modified equivalent of the reptilian quadrate."

Whatever may be the ultimate verdict on this difficult question, it is quite evident that among the theriodont anomodonts there must have existed forms in which the quadrate bone had more or less completely lost its articular function, and in which the two branches of the lower jaw had well-nigh discarded all their separate elements situated posteriorly to the dentary.

The mode in which this transition from the reptilian to the mammalian type has been effected is practically demonstrated by specimens figured in Dr. Broom's paper. The quadrate, according to the author's interpretation, forms a small knob to the descending process of the squamosal in the theriodonts, and has

<sup>1</sup> Dr. Kjellburg, in *Gegenbaur's Morphologisches Jahrbuch* for 1904.

<sup>2</sup> *Proceedings Zool. Soc. London*, 1904, vol. i., p. 490.

disappeared as a functional element in the mammal. In the true theriodonts the dentary element is much larger proportionally than in ordinary reptiles ; and while in *Lycosuchus* the surangular, angular, and articular elements of the hinder part of the lower jaw are fairly well represented, in *Cynognathus* the former has vanished, and the two latter are evidently on the point of following its example. In the words of the author :—

“The examination of the theriodont lower jaw and of its mode of articulation show that the condition is already so nearly mammalian that only a very slight modification, and that very easily understood, is required to convert the theriodont lower jaw into that of the mammal.”

In certain of the earlier and most primitive types of reptiles, such as *Pariasaurus* and *Procolophon* among the mammal-like group, the upper surface of the skull is more or less completely roofed in by superficial, or membrane, bones, so that, as in the former of these, the only apertures in this roof are those for the eyes, the nostrils, and the median parietal (or interparietal) foramen. In this respect the skulls of these primitive types resemble those of the primeval salamanders, or labyrinthodonts (*Stegocephalia*). On the other hand, more advanced types show a gradual opening-out of this roof, as if portions had been cut away with a knife, till finally the whole of the upper surface of the cranium proper is exposed. In some cases a single temporal arch, as in the Anomodontia, Chelonia, and Sauropterygia, remains to protect and strengthen the lateral region of the skull, but more generally, as in Crocodilia and Rhynchocephalia, there are two such temporal arches, with a space between. The accompanying illustrations show the closed and open types of skull. Among the more specialised orders, the Ichthyopterygia retain to a large extent the original in-roofing of the skull. It should be added that in the labyrinthodonts the upper surface of the skull displays a characteristic sculpture, which is retained in *Pariasaurus* and possibly also in crocodiles.

With regard to the above-mentioned parietal foramen, which occurs in many reptiles, and attains unusually large dimensions in the tuatera and the ichthyosaurs, it should be explained that this is a perforation in the forehead between

the two parietal bones which communicates with that region of the brain known as the epiphysis. It is also present in the primeval salamanders ; and in the tuatera overlies the remnants of an aborted and degenerate eye. From a certain want of symmetry in this structure in the tuatera it has been inferred



FIG. 1.—A, Upper surface of skull of a Labyrinthodont Amphibian to show the roofed type. B, Upper surface of skull of Tuatera (*Sphenodon*) to show open type. C, Front view of the lower end of the tibia of a bipedal Dinosaur with the closely applied astragalus. The hole in *Pt.* is the parietal foramen.

that the parietal eye was originally double ; and that ancestral vertebrates were furnished with a pair of such eyes, which may have been serially homologous with the single pair of their descendants. It should, however, be added that no creature has hitherto been discovered whose skull exhibits apertures for this hypothetical second pair of eyes.

In regard to limbs, it would appear that reptiles were originally four-footed creatures, with five toes to each foot. In

the specialised and comparatively modern group of Squamata there is, however, a great tendency to the reduction of one or both pairs of limbs, this tendency culminating in the snakes, in all of which the limbs are altogether wanting, although represented by slight internal and external vestiges in certain families. Except in the more primitive types, the limbs of reptiles exhibit great plasticity, so that in many cases they become profoundly modified in accordance with the needs of adaptation to special modes of life.

A feature in the tarsus of all the members of the bird-like brigade (*Ornithomorpha*) is that the ankle-joint occurs between the upper and lower rows of small bones forming that segment of the skeleton, and not, as in mammals, between the upper row of the tarsus and the lower ends of the tibia and fibula. But this is by no means all, for in certain dinosaurs which habitually assumed the upright posture the astragalus and calcaneum, forming the upper part of the tarsus, become closely applied to the tibia and fibula so as to form practically a single bone with each. Moreover, the tibia, with the closely applied astragalus, may become the sole functional bone of this segment of the limb. In the figured specimen the astragalus sends up only a short process in front of the tibia, but in other instances, as in *Dryptosaurus*, this process becomes much larger and is in fact practically similar to that of the astragalus of birds, which in the adult condition becomes indissolubly fused with the tibia. Furthermore, in certain dinosaurs with three toes the three supporting metatarsal bones become closely applied to one another and likewise to the lower row of tarsal bones (reduced to two in number), thus combining, at all events occasionally (? pathologically) to form a cannon-bone corresponding to the tarso-metatarsus of birds. And yet even this extreme instance is but a case of parallel adaptive modification for the same end (namely, the assumption of the upright posture), for it seems quite evident that these dinosaurs were not the ancestors of birds. Nevertheless other reptiles with a tibio-tarsus and a tarso-metatarsus, or, what is the same thing, birds with a separate tarsus and disunited metatarsals, must once have existed.

Whether in the tarsus of the mammal-like brigade the ankle-joint normally occurred between the upper and the lower rows

of that segment, does not seem to have been ascertained. But here, again, it is clear that there must either have been some theromorphs with a mammal-like tarsus, or mammals with a tarsus of the reptilian type.

As regards other features of the skeleton, it may be noted that a true sternum, or breast-bone, exists, and that in many instances the ribs are furnished with uncinate processes, that is to say from the posterior side of each rib proceeds an oblique process which overlaps the succeeding rib. These same uncinate processes occur in birds, and may be inherited from reptiles.

The few features of the soft parts of reptiles to which space permits of allusion may be very briefly dismissed, since it is generally impossible to say whether they were common to the extinct types. Firstly, it is important to mention that epidermic scales—or their equivalents, large horny plates—form the characteristic covering of reptiles, and that the feathers of birds and the hairs of mammals are alike conspicuous by their absence. Here, in connection with the evolution of birds from reptiles, a great difficulty presents itself, for it seems almost impossible to imagine a scaly bird, while if we are driven to postulate a feathered reptile we are confronted with the difficulty of assigning an adequate reason for the development of such a type of covering. Less difficulty is connected with the idea of a scaly mammal, or even of a hairy reptile.

Cold blood is characteristic of all living reptiles, as is also the fact that the corpuscles of this fluid (like those of birds, but not of mammals) are furnished with a nucleus. The heart is in the main tripartite, but of such a type that the four-chambered organ of both birds and mammals might be easily evolved therefrom. Similarly, the presence of a right and a left aortic arch, permits us to see how, by the suppression of one or the other, the mammalian and the avian type of circulatory system have been respectively evolved. The gills of the young of the ancestral amphibians have been completely lost in reptiles so that, as in the two higher vertebrate classes, respiration, takes place by means of lungs alone. The excretory organs, as in birds and the lower mammals, discharge into a common outlet—the cloaca. During development the embryo is enveloped in the two membranes respectively known as the amnion and the allantois; and the egg is of what is termed the

meroblastic type, that is to say, only a part of its contents segments and enters directly into the formation of the embryo, the remainder serving as nutriment to the latter in later stages of its development. In both these respects reptiles differ from amphibians and resemble birds; and it can scarcely fail to be noticed that throughout the organisation of the existing members of the class under consideration there is not a single feature which militates against their having been derived from amphibians, or it may be added, against their having given rise to birds on the one hand and to mammals on the other.

## CHAPTER II

### PEDIGREES AND RELATIONSHIPS

Reptiles and their relationship to warm-blooded Vertebrates: the origin of reptiles. The Theromorpha and their relation to the Mammalia: the Ornithomorpha and their relation to birds. The tuatara: crocodiles and their ancestry: tortoises and turtles: flying reptiles: dinosaurs: snakes and lizards: geological history: plesiosaurs and ichthyosaurs: numerical strength.

**I**N the preceding chapter it has been mentioned that reptiles appear to have given rise on the one hand to mammals and on the other to birds; they are thus the parental stock of all warm-blooded vertebrates. Modern authorities are generally agreed that reptiles themselves are derived from the primeval salamanders, or stegocephalian amphibians, and that the evolution of the class took place during or about the Lower Permian period, that is to say towards the close of the Palaeozoic era. There is, however, some difference of opinion as to whether the origin of reptiles from amphibians was single or dual (monophyletic or diphyletic), and also as to the exact limitations of the two classes. Dr. H. Gadow, for instance, in the *Cambridge Natural History* includes in the Reptilia certain Permian forms, such as *Eryops* and *Cricotus*, which are usually regarded as stegocephalian amphibians, to form a group termed the Proreptilia, which is regarded as the starting-point from which all true reptiles have sprung. He also classes as reptiles the so-called Microsauria, which are likewise generally considered to be stegocephalians, brigading them with the Rhynchocephalia (*Protorosaurus*, *Sphenodon*, etc.) to form a group—Prosauria—connecting the Proreptilia with other reptiles. He thus postulates a monophyletic origin for the Reptilia in general.

On the other hand, another authority, Mr. G. A. Boulenger, in an article published in the *Proceedings* of the Zoological Society of London for the year 1904 refused to admit Dr. Gadow's Proreptilia and the Microsauria into the class of

reptiles, for which he suggests a dual origin from two distinct groups of the Stegocephalia, namely the Labyrinthodontia on the one hand, and the Microsauria on the other.

Although in one sense such diversities of opinion are a matter for regret, yet like political parties, they have their advantage, for in this particular instance they tend to show, even in the present crude and imperfect condition of our knowledge, the existence of a kind of border-land, or "buffer-state," between stegocephalian amphibians and reptiles, some of the inhabitants of which may be referred to the one or the other of these groups according to the idiosyncracy of the particular writer who may be attempting their classification.

Assuming, then, that we are right (following Mr. Boulenger) in dividing reptiles into two main divisions, or brigades, it may be considered not improbable that while the mammal-like division (*Theromorpha*) may trace its origin to the Labyrinthodontia, the bird-like brigade (*Ornithomorpha*) may have sprung from the Microsauria.<sup>1</sup>

The Theromorpha, which appear to be confined to the Permian and Triassic periods, are connected with the labyrinthodonts by means of the Pariasauria, as represented by the huge amphibian-like reptiles from the Trias of Africa and Russia constituting the genus *Pariasaurus*. In this group the skull was as completely closed in by roofing bones as in the labyrinthodonts (Fig. 1), but its under surface had lost the parasphenoid bone characteristic of amphibians in general. From *Pariasaurus* there is a transition in one direction to the Ctylosauria, as represented by *Pariotichus*, *Empedias*, *Diadectes*, *Pelerpetum*, and *Procolophon* which still have the temporal region of the skull more or less completely roofed over with bone, but which differed from the Pariasauria by the greater number of joints in the toes. Some of these reptiles, it may be remarked, had the cheek-teeth expanded transversely, which suggests kinship with mammals, despite the fact that the group appears to have died out without descendants, being merely a side-branch from the Pariasauria.

On the other hand, the latter group appears to have also given rise to the Anomodontia, which apparently included, in

<sup>1</sup> Since this was written fuller details as to the relationships of the Microsauria have been published by Mr. R. S. Moodie.

MARS

SKELETON OF PARIASAURUS, THE ANCESTRAL TYPE OF THE MAMMAL-LIKE REPTILE.



the form of the Theriodontia, the ancestors of mammals, and are characterised, among other features, by the opening-up of the temporal region of the skull, with, as already mentioned, the formation of a single temporal arcade, which, however, at least in some cases, as *Cynognathus*, for example, consists of two elements.

To describe in detail the mammalian features presented by the anomodonts and other Theromorpha, or indeed the general characteristics of that subclass, would be out of place on the present occasion. It may be mentioned, however, that the skull, with the exception of the retention of a quadrate, a compound lower jaw, and a prefrontal bone (which is a characteristic reptilian feature) in many cases might almost be described as that of a mammal. The reduction in the size of the quadrate and of the posterior elements of the lower jaw in this group has been already noticed. In the theriodont, or carnivorous, section of the anomodonts, as exemplified by *Cynognathus* and *Galecynus*, the teeth recall those of carnivorous mammals. The shoulder and pelvic girdles are also essentially of the same type as those of the monotreme, or egg-laying, mammals, and present, moreover, a remarkable serial homology; that is to say, the three elements of the one (scapula, epicoracoid, and coracoid) correspond almost exactly with those of the other (ilium, pubis, and ischium) while the obturator foramen, or perforation between the pubis and ischium is an essentially mammalian feature. Nor is this all, for the theromorph shoulder and pelvic girdles are essentially unlike those of other reptiles, this being especially the case with the pelvis, in which among many reptiles, such as dinosaurs, the pubis and ischium, are long divergent rods.

The humerus, or upper arm-bone, is also essentially like that of the lower mammals, having a strongly developed deltoid or radial crest in its upper half, and a perforation (entepicondylar) on the inner, or ulnar, side of its lower extremity. Not less important is the fact that the number of joints in the toes, at least in several cases, is the same as in mammals; while it would seem that, as in that group, the ankle-joint was situated between the tibia and fibula and the first row of the tarsus.

In concluding these observations on the relations between reptiles and mammals, the following passage from a paper

published by Professor H. F. Osborn in the *American Naturalist* for 1898 may be quoted:—

"Important, also, among the resemblances between the Theriodontia and Mammalia is the general bodily form, so far as it is known in the former, the proportions of the limbs to the back, and the apparent elevation of the body considerably above the ground. This, taken together with the peculiar specialisation of the teeth into carnivorous and herbivorous types, indicates that the Theriodontia filled somewhat the same rôle in the economy of nature as is filled by the Mammalia at the present time. The most striking general difference is the very large size of several of these animals, such as *Cynognathus*. We had rather anticipated from our knowledge of the earliest Stonesfield (Lower Jurassic) mammals that their reptilian ancestors would have been very small. The large size of these Permian (or Triassic) theriodonts is, however, not incompatible with the hypothesis that smaller and less specialised members of the group may have constituted a persistent phylum (or branch)."

Passing on to a proportionately brief survey of the probable evolutionary history of the numerous ordinal groups included in the subclass Ornithomorpha, it may be repeated that the most primitive and at the same time the most ancient of these orders is undoubtedly the Rhynchocephalia, which includes the Permian *Protorosaurus*, and may have sprung directly from the microsaurian amphibians. The Rhynchocephalia, now surviving only in the form of the New Zealand tuatara (*Sphenodon punctatus*, Plate II.), are characterised, among other features, by the presence of complete upper and lower temporal arcades to the skull, which also shows a large parietal foramen, by the bodies of the vertebrae being cupped at both ends, by the presence of intercentra between many of the vertebrae, and of chevron-bones attached to the lower surface of those of the tail, by the fully developed shoulder-girdle and five-toed limbs, the firmly fixed quadrate bone, the acrodont teeth, and the presence of a foramen (entepicondylar) on the inner side of the lower end of the humerus, and of a system of abdominal ribs, forming an incipient plastron on the lower surface of the body. Of the numerous divergent branches which have been given off from the rhynchocephalian stock, one has apparently culminated in the birds. Among the fossil representatives of the group may be

mentioned *Palaeohatteria* of the Lower Permian of Saxony, a long-tailed reptile of about a foot and a half in length, and the aforesaid *Protorosaurus* of the Upper Permian of Thuringia and Durham which attained a length of between four and five feet. These are the earliest and most primitive types. More nearly allied to *Sphenodon* is *Rhynchosaurus* of the Upper Trias, or Keuper, of Shropshire and Warwickshire, and *Hyperodapedon*, with its pavement-like series of upper teeth, from the Upper Trias of both England and India. Much nearer to the living type is *Homaeosaurus* of the Upper Jurassic of the Continent; while in the Upper Cretaceous the group is represented by the long-snouted *Champsosaurus*. Very interesting is *Proterosuchus* of the South African Trias, which appears to be a rhynchocephalian showing a considerable degree of specialisation along the line which gave rise to the crocodiles.

Very few words must suffice for the Pelycosauria, a group of chiefly North America Permian reptiles, whose affinity seems to be with the Rhynchocephalia, from which they apparently form a side-branch. They have frequently been confounded with the theriodont anomodonts, to which they assimilate in their dentition. The quadrate-bone is remarkably small and surrounded by the adjacent elements ; and in the typical forms, such as *Naosaurus*, the spines of the dorsal vertebræ, as will be more fully noted in the sequel, are enormously elongated. The dentition is thecodont.

Next in the direct line of descent from the rhynchocephalians may be placed the Upper Triassic belodonts, or Paracochlia (sometimes, although incorrectly, termed Thecodontia). These reptiles, as typified by *Phytosaurus* (or *Belodon*), are frequently classed with the crocodiles, with which they agree in having the teeth set in distinct sockets, and in possessing a pitted dermal bony armour ; the teeth, as in crocodiles, having hollow roots in which the germs of their successors are developed, like a "nest" of thimbles. As a matter of fact, the belodonts appear to be equally nearly related to a number of others. They resemble, for instance, pelycosaurians, typical dinosaurs, and crocodiles in their socketed teeth ; and thereby differ markedly from rhynchocephalians. On the other hand, they agree with the latter group and with pelycosaurians, and differ from crocodiles and dinosaurs in the retention of distinct

clavicles, or collar-bones ; and also approximate to the rhynchocephalian type in their system of abdominal ribs. A marked difference from crocodiles is to be found in the circumstance that three elements of the pelvis (ilium, pubis, and ischium) enter into the composition of the acetabular cavity for the reception of the head of the thigh-bone, or femur—a generalised feature they possess in common with dinosaurs. *Phytosaurus* itself was a reptile of the dimensions of a good-sized crocodile, with an enormously long snout, at the base of which opened the nostrils.

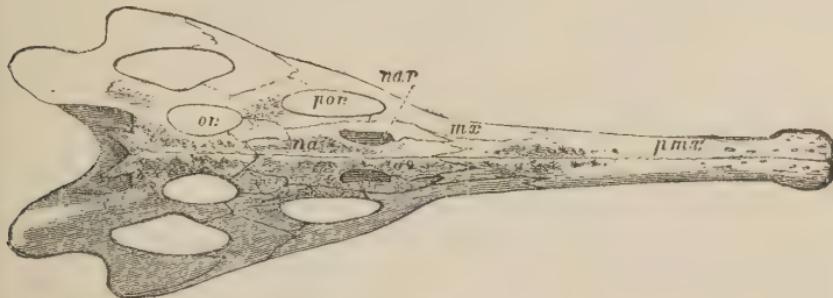
The belodonts are remarkably interesting reptiles, for in a provisional genealogical tree published in the Zoological Society's *Proceedings* for 1904 they occupy the intermediate position between rhynchocephalians and birds, being placed, however, much closer to the former than to the latter group. As a matter of fact, we know at present nothing in any way intermediate between belodonts and birds, between which there is evidently a very long gap ; and we are consequently totally ignorant of the mode of evolution of the many peculiarities in a bird's skeleton. Not that this affords any argument against the evolution of birds from reptiles, any more than does the fact that we are ignorant of the direct ancestors of the pterodactyles, and consequently the mode of evolution of the skeleton of their wings.

There are several notable features in the skull of the belodonts, in addition to the backward position of the opening of the posterior nostrils. In the first place, the comparatively small size of the apertures in the temporal region is a primitive feature, very different from what obtains in the crocodiles as shown in the figure of the skull of *Metriorhynchus*. A second feature is the great length of the premaxilla, which is also in marked contrast to what obtains in crocodiles.

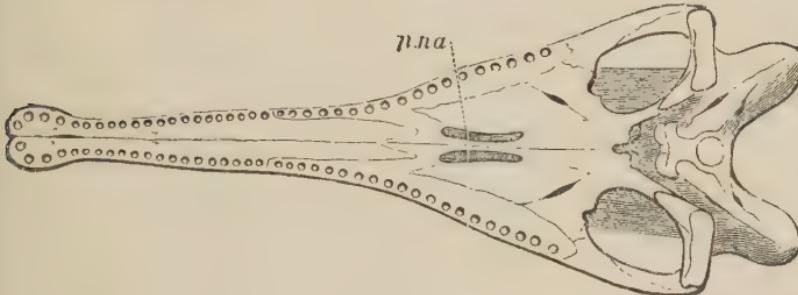
Reverting to the Parasuchia as a starting-point, we may probably regard the ichthyosaurs (Ichthyopterygia) as a side branch from this stock, in which specialisation has been concentrated on the needs of an aquatic existence. Ichthyosaurs agree with belodonts in their complete clavicles, but their teeth are implanted in grooves, and evidence of kinship with stegoccephalian amphibians is manifested in the retention of a partial roof to the temporal region of the skull. Another early side

branch from the belodonts is that of the crocodiles which retain the dermal armour and socketed teeth, but have lost their clavicles and the pubis has become excluded from the acetabular cavity of the pelvis. Specialisation early displays itself

A



B



C

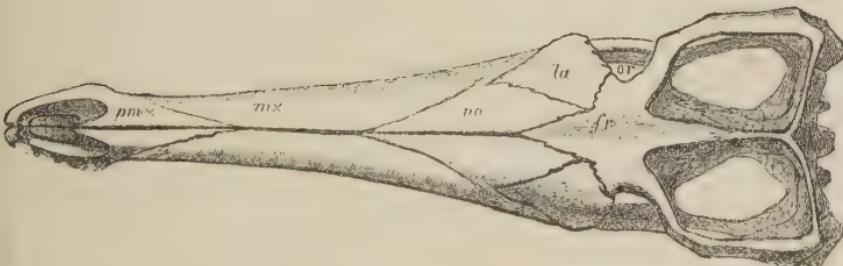


FIG. 2.—Upper (A) and lower (B) views of the skull of a Belodont (*Phytosaurus*) a primitive reptile from the Upper Trias : nar. nostrils; p. na. posterior nostrils; pmx. premaxilla. C. Upper view of skull of an extinct Crocodile (*Metriopnynchus*) to show the open temporal region and the small premaxillæ as contrasted with the corresponding parts in *Phytosaurus*.

In the backward transference of the posterior openings of the nostrils into the mouth, by means of the development of a false floor to the palate of the skull, but it was not until the Tertiary period that this feature obtained its full development. The culmination of this adaptive modification was attended by the

development of ball-and-socket (instead of nearly flat or slightly hollowed) articulations to the vertebræ ; the socket being in front and the ball behind, thus constituting the procœlous type of vertebral structure.

From a branch arising directly from the rhynchocephalian stock, without the intervention of the belodonts, may probably be derived plesiosaurs (*Sauroptrygia*) and tortoises and turtles (*Chelonia*) ; these two orders having many points in common, such as a single (upper) temporal arcade, a fixed quadrate-bone, the mode of articulation of the ribs to the vertebral column, and the presence of clavicles, and of either a true plastron or a system of abdominal ribs. Specialisation has, however, taken different lines in the two groups : in the one case the protection of the body in a shell, together with the loss of the teeth ; while in the other socketed teeth are retained, and the limbs in the more specialised forms become modified into paddles. Although the plesiosaurs can be traced downwards into terrestrial or fresh-water forms, we are at present quite ignorant of the ancestry of the chelonians.

The placodonts, or bean-toothed reptiles (*Placodontia*) of the Trias, were long regarded as members of the theromorphous, or mammal-like brigade, but a later view is to consider them as members of the branch which gave rise to the chelonians and plesiosaurs, with both of which they agree in the general characters of the skull, while they resemble the latter in their socketed teeth. A peculiar feature, as will be noticed later, is the extension of the teeth on to the palate, and their crushing type of crown.

A totally independent branch from the main stem is formed by the pterodactyles, or flying reptiles (*Ornithosauria*), the whole of whose organisation is profoundly modified for the purpose of aerial flight. Pterodactyles retain evidence of affinity with the ancient parasuchian (and thence with the rhynchocephalian) stock in the retention (except in the more specialised forms) of socketed teeth, fixed quadrates, double temporal arcades, and distinct clavicles. Although the group cannot at present be traced into direct connection with terrestrial, non-volant reptiles, it is quite clear that it has nothing to do with birds.

The branch which has given rise to the largest of all reptiles is that of the Dinosauria, which, in the opinion of some author-

ties, ought to be split into two separate orders, namely the Dinosauria proper, as typified by the carnivorous and thecodont *Megalosaurus* and its allies, and the Orthopoda, to include the herbivorous types, in which the teeth have more or less completely lost the original socketed character. Whichever view be adopted, it is evident that all these reptiles are very closely related, and that it is the carnivorous group which connects them with the belodonts (Parasuchia). With that group dinosaurs agree in their double temporal arcades, fixed quadrates, and the inclusion of the pubis in the acetabular cavity of the pelvis, although they have lost the clavicles. The more specialised dinosaurs, like crocodiles, have developed ball-and-socket articulations to the vertebræ, but it is remarkable that the positions of the balls and sockets are just the reverse of those in the latter group, the socket being at the hind and the ball at the front end of the vertebral column, thus forming the opistho-coelous (in contradistinction to the procœlous) type of vertebral structure.

A few words may be devoted in this place to the supposed direct phylogenetic relationship between birds and dinosaurs. When the many curious resemblances undoubtedly existing between the bones of the pelvis and hind-limbs of those dinosaurs which habitually assume the upright posture, such as the incipient union between the lower end of the tibia and the astragalus, and the consequent tendency towards the formation of a tibio-tarsus and a tarso-metatarsus, were first brought to light, it was confidently assumed that dinosaurs represented the ancestral stock from which birds had originated. This view was strengthened by the fact that primitive birds were furnished with teeth implanted in sockets after the megalosaurian type. Neither was it weakened by the circumstance that birds have a free quadrate-bone and only a single (lower) temporal arcade; the loosening of the attachment of the quadrate being doubtless correlated with the loss of the upper temporal arcade. A more serious, although not insuperable objection, is the retention of clavicles by birds.

When, however, the doctrine of parallelism in development, owing to structural adaptations for more or less nearly similar modes of life, became generally recognised as a powerful factor in the evolution of animals, opinion veered in the opposite

direction, and it was considered by many high authorities that the resemblances existing between the pelvic and limb skeletons of dinosaurs and birds were solely the result of adaptation, and were not indicative of genetic relationship between the two groups. It is true, that a guarded protest was raised by the celebrated American palaeontologist Professor H. F. Osborn in a paper published in the *American Naturalist* for 1900. In this communication it was remarked that the passage from a quadrupedal to a bipedal mode of progression would mark the transition from the protorosaurian rhynchocephalians (the admitted ancestors of the ornithomorphous brigade of reptiles) to dinosaurs, and consequently "that our present knowledge and evidence justify us in saying that in this bipedal transition, with its tendency to form the tibio-tarsus, the avian phylum may have been given off from the dinosaurian".

Later opinion has, however, on the whole been markedly against this partial reversion to the older theory of the descent of birds from dinosaurs. Another well-known authority, Dr. H. Gadow, points out, for instance, in the volume on reptiles in the *Cambridge Natural History* that those dinosaurs which exhibit the most marked avian resemblances did not come into existence until about or after the time that birds had been fully differentiated. After putting these later types out of court, the author proceeds as follows:—

"There remains only *Anchisaurus* of the Upper Trias, more or less contemporary with *Brontosaurus*, which left its three-toed foot-prints (*Archæopteryx*<sup>1</sup> has four well-developed toes) with *Zanclodon*. Moreover, the most bird-like foot is either that of the Theropoda [*Megalosaurus*, etc.] which, like *Anchisaurus* and *Zanclodon*, differ from birds by the formation of the pelvis, or of some of the latest Ornithopoda [*Iguanodon*, etc.]. What, then, is the good of selecting a number of bird-like features from members of dinosaurs which we are bound to class in different groups, and which existed, some in the lower, others in the middle, or even in the latest Mesozoic periods?"

Dr. Gadow's contention appears to receive support from the British Museum specialist on reptiles, Mr. G. A. Boulenger, who, in a paper in the *Proceedings of the Zoological Society* for 1904, to which reference has been already made, derives

<sup>1</sup> The toothed and long-tailed Upper Jurassic bird.

dinosaurs from a side branch of the stem connecting belodonts with birds. According to this view the proximate reptilian ancestors of birds still remain to be discovered. Possibly it was in Africa that the annexant forms were developed.

The last branch of the Reptilia is the one culminating in the Squamata (snakes and lizards), which, like plesiosaurs and chelonians, appears to be directly derived from the primitive rhynchocephalian stock, with which it is connected by means of the Acrosauria, a group provisionally admitted to ordinal rank, and typified by the lizard-like *Acrosaurus* and *Pleurosaurus* of the Upper Jurassic of the Continent. The Squamata have either retained the ancestral acrodont dentition of the Rhynchocephalia, or have modified this into the pleurodont type. They have also inherited the ancestral clavicles; but, on the other hand, they have completely discarded the rhynchocephalian plastron, or abdominal ribs and also the uncinate processes of the true ribs. They have likewise lost the lower temporal arcade, that is to say, the one connecting the quadrate by means of the quadrato-jugal and jugal with the maxilla; and probably correlated with the loss of this bar is the loosening of the attachments of the quadrate itself, which is movably attached to the skull, and thus makes a loose hinge for the lower jaw, which is of special value to the pythons, boas, and other snakes which gorge their prey in bulk. The complete scaling of the body is, as its name implies, a very characteristic feature of the order, although in some cases this has been lost.

Next to fishes and amphibians (as represented by the Stegocephalia), reptiles are the oldest vertebrates; in other words, they are the oldest of the amniotic vertebrates. Bearing this in mind, and also remembering the fact that (unlike fishes, which are restricted to the water) during the Mesozoic epoch they alone filled, in the main, the places now occupied in nature conjointly by terrestrial and aquatic mammals, birds, and reptiles, it is not surprising to find that, with the progress of time, they have lost more heavily in ordinal groups than any other vertebrate class. They have, in fact, been much more than decimated, for out of the fifteen orders recognised in the table on page 4 only four, as already said, now exist, and of these one is represented only by a single genus and species, or, at most, by two or three closely allied species of that genus.

Of the various groups of reptiles, the entire subclass Theromorpha appears to have been confined to the Permian and Triassic periods; its oldest known representatives being probably those from the Permian of Texas. Whether the latter strata are somewhat older or newer than (it is unlikely that they are the exact equivalent in age) the Lower Permian of Europe, cannot be determined; and it is therefore impossible to say whether the Theromorpha are older than Ornithomorpha, or *vice versa*. Be this as it may, the Theromorpha, as represented by the Pariasauria, probably originated from the labyrinthodont stegocephalians in the Permian, or, at all events, in the later Carboniferous; while the Theriodontia probably gave rise to mammals in the Trias. Having achieved this triumph, their task appears to have been accomplished, and they gradually waned and finally disappeared from the scene. Previous to, or about, the time that they gave rise to the Mammalia, the Theromorpha appear to have been the dominant forms of terrestrial vertebrate life, the contemporary rhynchocephalians, like most of their successors, being comparatively small creatures. For a long period their descendants the mammals were, however, at least over a large part of the world, in a subsidiary position; and did not in fact regain the inheritance of those reptilian ancestors as the lords of creation till the Tertiary period.

Turning to the second, or bird-like brigade (Ornithomorpha), we find that the most primitive order, namely the Rhynchocephalia, is the most ancient, or, at all events, as ancient as the nearly related Pelycosauria (on the supposition that it is the ancestor of all the class, it must of course be the oldest). As already said, its oldest known representatives are *Paleohatteria* of the Lower Permian and *Protorosaurus* from a somewhat higher stage of the system; the presumed evolution from the microsaurian stegocephalians having probably taken place in either the Lower Permian or the Upper Carboniferous. In the Trias the rhynchocephalians were well represented, and they are known by several forms from the Jurassic, while there is evidence of their existence in the Cretaceous. The links between the Jurassic forms and the existing New Zealand species are, however, still unknown, and may not improbably have flourished in southern lands which have long since been sub-



THE NEW ZEALAND TUATERA (*SPHENODON PUNCTATUM*) THE SOLE SURVIVOR OF THE MOST PRIMITIVE AND MOST ANCIENT GROUP OF THE BIRD-LIKE REPTILES  
TOTAL LENGTH ABOUT 15 INCHES



A GIRDLE-TAILED LIZARD (*ZONURUS GIGANTEUS*) OF SOUTH AFRICA, TO SHOW APPARENT SIMILARITY OF LIZARD AND TUATERA



merged. The Pelycosauria, which, as already said, formed a specialised side branch from the rhynchocephalian stock, appear to have waxed and waned within the duration of the Permian period, when they were represented on both sides of what is now the Atlantic.

The mantle of the Rhynchocephalia may be said, however, to have fallen on the Squamata (lizards and snakes), which is at the present day the most numerously represented of all reptilian orders, holding a position in the class analogous to that occupied by the perching birds in the class Aves. Here, then, we may trace a parallel as regards evolutionary history between the anomodonts on the one hand and the rhynchocephalians on the other. As mammals—the descendants of the anomodonts—after passing through a long epoch when they were, so to speak, under a cloud, eventually rose to pre-eminence, so the Squamata, after a period of subordination, eventually attained the dominant position among reptiles of to-day. If we regard birds as likewise the direct descendants of the rhynchocephalians, the parallelism between that group and the anomodont-mammal line is still more remarkable.

As to the epoch when the rhynchocephalian type blossomed out into that of the Squamata we are still in the dark. If the Acrosauria formed the connecting link, the evolution must have been during or later than the Upper Jurassic. Squamata are known from the Cretaceous, but as these (*Dolichosaurus*) are marine types they almost certainly imply the existence of earlier terrestrial forms, unless indeed they be independently derived from the aquatic rhynchocephalian *Champsosaurus*. From the early Tertiary remains of both lizards and snakes are known: and since the Egyptian Lower Eocene *Gigantophis cromeri* was of very large size, it is practically certain that there were earlier types of inferior dimensions.

The belodonts, or Parasuchia, appear to have been solely of Triassic age. The ichthyosaurs, on the other hand, ranged from the Trias to the Upper Cretaceous, and may possibly have survived in some parts of the globe into the earliest Tertiary. Even the Triassic forms appear to have been marine, and we have consequently yet to find the connecting links between this group and earlier reptiles. The members of this order had attained their maximum development in point of size as early

as the Lower Lias; but as some of the Cretaceous more specialised species were equally large, the dying-out of the group seems to have been sudden, as there is no sign of decadence or degeneration. The cause of this apparently sudden extermination is altogether beyond our ken!

The geological history of the plesiosaurs (*Sauroptrygia*) is very similar to that of the ichthyosaurs, except that the Triassic types were smaller and more nearly akin to terrestrial forms, and that the largest species occurred in the Upper Jurassic and Cretaceous periods, although some of those from the Lias were gigantic. The small group of placodonts (*Placodontia*) appears to have been solely Triassic.

Chelonians, as represented by *Proganochelys* and *Chelytherium*, date from the Upper Trias, but these forms are as typically chelonian as is any modern tortoise, so that we have evidently to go further back before the order can be traced to the ancestral stock. From the Trias chelonians appear to have steadily increased in numbers to the present day, when they form the second largest reptilian order. The Chelonia of the Jurassic strata belong to a generalised group known as the Amphichelidia, from which appear to have diverged the modern *Cryptodira* and *Pleurodira*, of which the latter is now on the wane. The origin of the soft-tortoises, or *Trionychoidea*, is unknown, but they were abundant in the early Tertiary, and also occur in the Upper Cretaceous. True marine turtles (*Chelonidae*) also date from the Upper Cretaceous, and were preceded by ancestral forms in the Upper Jurassic. Upon the question whether the Triassic *Psephoderma* is really chelonian or not, largely depends the problem as to the nature of the relationship between the true turtles (*Chelonidae*) and the leathery turtles (*Dermochelyidae*) of our modern seas.

The pterodactyles, or Ornithosauria, according to our present information, date from the Lower Lias and continued right through the overlying Mesozoic formations. Since, however, their earliest known representative—*Dimorphodon macronyx* of the Lower Lias of Dorsetshire—is in all respects a typical and fully evolved member of the group, it can scarcely be doubted that their origin must be looked for at an earlier epoch of the earth's history. Beyond the fact that some of the more specialised forms of the later formations have lost

their teeth and diminished the length of the tail, it can scarcely be said that the group exhibits much signs of progressive evolution above its Liassic prototype. Indeed, there is no reason that it should, seeing that the species in question appears to be thoroughly adapted in every particular for a life in the air and predatory habits. In some of the gigantic Cretaceous forms alluded to in the sequel, specialisation, in correlation with the enormous dimensions of the wings, shows itself in the welding of the scapula to the dorsal vertebræ. Another form of specialisation is shown by the development of a ring of bones in the eye.

The dinosaurs (*Dinosauria*), like the ichthyosaurs and plesiosaurs, commenced in the Trias and continued to flourish till the close of the Cretaceous period, when some of their members, as is more fully noticed in the sequel, underwent some most strange and bizarre developments. It is specially important to notice that all the known Triassic forms belong to the typical carnivorous group (*Dinosauria proper*), commonly known as *Theropoda*; the more specialised herbivorous types being a later development. It is largely on account of this fact that all the groups are included in a single order in the present work; although many naturalists prefer to consider the herbivorous forms as constituting an order by themselves. Another very remarkable circumstance is that some of the Triassic representatives of the order had already assumed the bipedal mode of progression. This early assumption of the erect posture makes it somewhat difficult to accept a theory suggested by Professor H. F. Osborn, of New York, to the effect that birds were probably an offshoot from the dinosaurian stock before the posture in question had been attained by any of the members of the latter. The huge herbivorous dinosaurs of the group *Sauropoda* are known to have been in existence in the early part of the Jurassic period (exclusive of the Lias); while the armoured, or stegosaurian, section of the second great herbivorous group (*Ornithopoda*) date from the Lower Lias; these Liassic forms being much less fully armoured than were the Jurassic and Cretaceous successors. The highly specialised iguanodonts date apparently from the Upper Jurassic and Wealden.

To attempt to make a census of the known forms of extinct reptiles would be, in the first place, a matter of extreme diffi-

culty, while, in the second place, if this were accomplished, it would be quite valueless. It would be difficult because the records are much scattered, and a number of generic and specific names have been assigned to specimens of so imperfect and unsatisfactory a nature that in many cases it is impossible to say whether or no they are mere synonyms. It would be valueless because the known forms of extinct reptiles must, from the very nature of the case, bear but a small proportion to the number of species that have existed. Nor is this all, for in order to make the census of the slightest use it would be necessary to divide these known forms into time-horizons, the number of which it would be extremely difficult to fix satisfactorily.

Neither, in the present state of zoological science, is a census of the existing members of the class altogether free from some degree of uncertainty; for very different views of the limitations of species are entertained by different naturalists. In accepting, however, the number of species given in the volumes of the British Museum Catalogues we shall certainly be on the safe side, as the author of the latest editions of such of those works as deal with reptiles is a naturalist who takes a broad view of the limitations of a species, and is not given to hair-splitting in this respect. It must be remembered, however, that these works are now somewhat out of date in respect to the number of known species of reptiles, the last volume of the catalogue of lizards having been published so long ago as 1887, while the one on crocodiles and chelonians was issued a year later, and the concluding volume of the snake-catalogue in 1896.

Taking, however, the data given in these volumes, we have the following numbers for the five chief divisions of existing reptiles, namely:—

Tuateras (Rhynchocephalia)	.	.	.	I
Crocodiles (Crocodilia)	.	.	.	23
Tortoises and Turtles (Chelonia)	.	.	.	201
Lizards (Lacertilia)	.	.	.	1616
Snakes (Ophidia)	.	.	.	1639

This gives a total of 2480 species, a number which, by subsequent additions to the list, may be safely increased to at least 2600.

Although this number largely exceeds that of the Amphibia (frogs, toads, salamanders, etc.), which was 633 in 1882, and now, perhaps, approaches 700, it is incomparably inferior to that of the other three great vertebrate classes. For instance, so long ago as the year 1870, Dr. A. Günther estimated the number of known species of fishes at 9000, and at the present day the estimate would be very much larger. As regards birds (in which, it should be observed, species are often separated on slight characters), the number in the passerine and "picarian" groups alone was given in 1900 as 6487. Of mammals (to which the same remark applies) considerably over 7000 species, inclusive of extinct forms, were catalogued in 1899 by Dr. E. L. Trouessart, and the number has since been increased.

One feature is very noticeable in all the five vertebrate classes, namely the predominance in point of numbers of one particular order or group at the present day; the great majority of the representatives of such orders being of comparatively small bodily size, although to a certain extent fishes and, among reptiles, snakes form exceptions in the latter respect.

Thus in the class Pisces we have the Teleostomi (bony fishes), in the Amphibia the Ecaudata (frogs and toads), in the Reptilia the Squamata (lizards and snakes), in Aves the Passeres (perching birds), and in Mammalia the Rodentia (rodents), as the overwhelmingly predominant group in point of numbers. Each one of these groups, it should be added, is of a highly specialised and essentially modern type.

## CHAPTER III

### HAUNTS AND HABITATS

The haunts of reptiles in past times, and at the present day. The sea-iguana. Dearth of reptiles in polar and sub-polar regions. Haunts of tortoises and snakes. Tree-dwellers. Burrowers. Island forms. Geographical distribution, difficulties of interpretation. Relation to temperature, moisture, etc. Hibernation and aestivation.

DURING the earlier and middle stages of their long and eventful history, when they were the dominant vertebrates other than fishes, reptiles, as will be more fully shown in the sequel, were adapted to occupy every station on the earth, and to fill every rôle in life. The ichthyosaurs and plesiosaurs, and later on the extinct sea-serpents (*Pythonomorpha*), together with numerous turtles and a peculiar group of crocodiles, were denizens of the ocean, in which the three first-named groups played the part now taken by whales in the scheme of creation.<sup>1</sup> The pterodactyles, or flying saurians, were, on the other hand, inhabitants of the air, where, so far as their power of flight permitted, they took the place now occupied by birds. It is, however, improbable that any of these creatures were adapted to a purely pelagic existence comparable to that of the albatross and the tropic-bird at the present; and, indeed, we do not even know whether they were capable of swimming on the surface of the sea after the fashion of modern sea-birds. Again, to what extent they were adapted to an inland life is likewise uncertain, the great majority of their remains having been obtained from shore-deposits, such as the Lias, although some have been found in the Chalk which was probably deposited in deeper water. It is true indeed that in the Stonesfield Slate of Oxfordshire remains of pterodactyles are found in association with those of mammals and other land animals, but

<sup>1</sup> The Middle Jurassic *Ophthalmosaurus* appears to have been more completely pelagic than any of the other ichthyosaurs.

this by no means implies that they themselves were dwellers in an inland district. As a matter of fact, the Stonesfield beds are a lagoon-deposit, into which the remains of land animals and plants were washed down by rivers; and the pterodactyles were probably inhabitants of the shores of the lagoon itself. This inference is supported by the fact that pterodactyle remains are unknown from the purely fresh-water and terrestrial deposits of the Dorsetshire Purbeck. Consequently, it seems probable that pterodactyles were in the main frequenters of coast-lines, and that they did not take the place of birds in inland districts. This is the more likely seeing that at any rate as early as the Upper Jurassic true birds (*Archæopteryx*) were already in existence.

On land, throughout the Mesozoic epoch, huge dinosaurs played the part of the great land mammals of the later Tertiary period and the present day; while rhynchocephalians, fresh-water tortoises, and crocodiles fulfilled the rôle of lizards and snakes and the modern representatives of the last-named group. Whether there were arboreal reptiles (other than pterodactyles) during the Jurassic and Cretaceous periods, we have no means of knowing.

At the present day all this predominance and exuberance of reptilian life have completely passed away. The dominion of the air, or such claim to the same as could be maintained by the pterodactyles, has been completely lost, not a single existing reptile having the power of true flight. Much the same may be said with regard to the "command of the sea" formerly possessed by the reptilian class, for at the present day there are no truly pelagic reptiles (if we except the mythical sea-serpent) save the sea-snakes, none of which exceeds five or six feet in length, and most of which are less. Turtles—both leathery and otherwise—are it is true in the main pelagic reptiles, but they go ashore to deposit their eggs, and are thus not comparable to ichthyosaurs and plesiosaurs on the one hand and to whales on the other. The only other reptiles which can in any true sense be called marine are the Indian *Crocodilus porosus* and the Galapagos sea-iguana (*Amblyrhynchus cristatus*); but these spend a large portion of their time on land, and the former is by no means exclusively a denizen of the coasts but is rather an amphibious land reptile which takes partly to a marine life. It should be

added that the great water-monitor (*Varanus salvator*) of India will, when frightened, occasionally rush headlong into the sea.

Apart from the air and the ocean, the reptiles of the present day have availed themselves of most stations suited to their mode of life over the greater part of the earth with the exception of the polar and sub-polar regions, although they attain their maximum development, both as regards bodily size and numbers, in the tropical and sub-tropical zones.

Rivers and lakes, for example, are inhabited by various kinds of fresh-water tortoises, belonging to several distinct groups, among which the soft-tortoises, or *Trionychidæ*, are exclusively aquatic, although they spend much of their time basking on sand-banks. Many snakes, too, such as the common British grass-snake (*Tropidonotus natrix*), the North American water-mocassin (*Ancistrodon piscivorus*), and the huge anaconda (*Eunectes murinus*) of South America, are in a greater or less degree aquatic; while several of the iguanas, and especially the basilisk (*Basiliscus americanus*) likewise spend much of their time in the water, as do some of the Old World monitor lizards.

A large number of reptiles have found safety from enemies and an abundant food-supply by taking to an arboreal life. Among such are the chamæleons, many geckos, a large number of iguanas, and many Old World lizards. Among the latter special attention may be directed to the so-called flying-dragons (*Draco*) of the Malay countries, on account of the membranous expansions by means of which they are enabled to take long flying leaps from bough to bough. Many snakes, such as the whip-snakes and the various kinds of tree-snakes, are wholly arboreal; while others, such as the pythons and boas, spend much of their time on trees. Certain snakes are also stated to take short journeys in the air, the natives of Borneo attributing the power of flight to *Chrosopelea ornata*, *C. chrysochlora*, and *Dendrophis pictus*; and it appears that these reptiles really can descend from a height in a manner analogous to that practised by flying-squirrels. In the ventral scales of these snakes there is a suture on each side, and by muscular contraction these scales can be drawn inwards, so that the whole lower surface becomes concave, and the body may be compared to a split bamboo.

Experiment has shown that the snake when made to fall from a height, descends with the body rigid, and that the line of fall is at an angle from the point of departure to the ground. It seems probable that the concave lower surface buoys the reptile up in its fall, since the fall of a split bamboo through the air is perceptibly slower than that of an undivided rod of equal weight.

Other reptiles have taken to a more or less completely burrowing and subterranean life, frequently with loss of the limbs, and sometimes more or less abortion of the eyes ; thus coming under the designation of what many writers are pleased to call degraded animals, which is, of course, merely another term for specialisation and adaptation in a particular direction. Among such burrowing and worm-like creatures are several families of snakes—notably the blind-snakes, or *Typhlopidae*—and the amphisbænas and slow-worms among lizards. Many other reptiles, such as the spiny-tailed lizards (*Uromastix*) and the tuatera (*Sphenodon*) are burrowers, but without “degradation” ; while among the skink lizards (*Scincidæ*) almost every gradation from a fully limbed to a limbless burrower may be observed.

Of the purely terrestrial forms other than burrowers, limitations of space preclude anything more than the very briefest mention in regard to haunts. It may be observed, however, that, unlike the smaller mammals, a very large number of forms—and notably the lizards of the genera *Agama* and *Lacerta*—are diurnal in their habits, and trust to escape from enemies by the lightning speed with which they retreat into the crevices of the rocks they frequent. Desert forms, on the other hand, of which there are many, probably trust largely to resemblance to their surroundings as a means of escaping detection by foes. A large number of lizards living among grass likewise owe their safety to a similar protective resemblance, as is more fully noticed in the sequel.

Up to a recent date no reptiles were known to have adapted themselves to an existence in caverns ; but about 1898 it was discovered that numbers of a species of *Coluber* frequent caves in the Selangor district of the Malay Peninsula, where they feed on bats by which the cave is tenanted. These snakes grow to eight or nine feet, and are paler-coloured than ordinary, while their colouring presents a remarkable resemblance to that of the walls of the cave ; at first sight, suggesting that the reptiles are

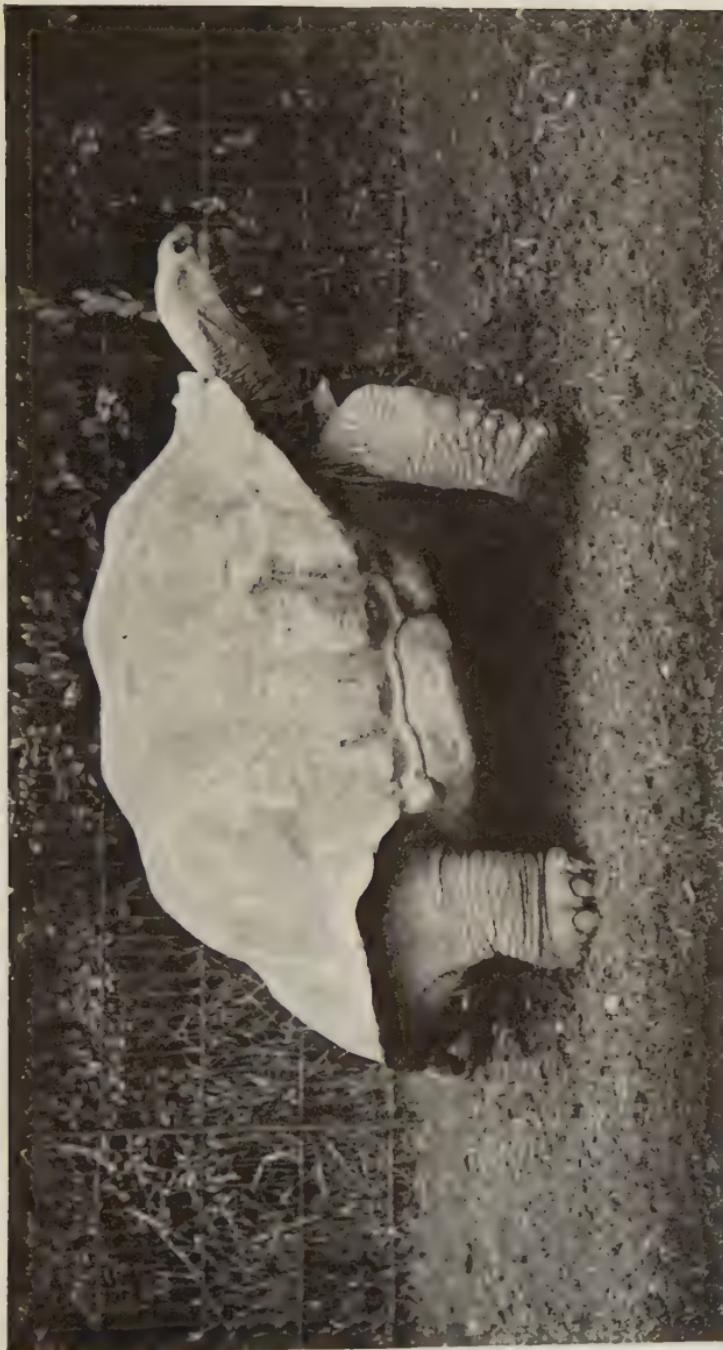
ancient cavern-dwellers. Such protective resemblance would be of no use when in the darkness of the inner parts of the cave, but many of these snakes are in the habit of taking up their quarters on ledges near the entrance, from which they seize the bats passing in and out. The cave-walls consist of yellowish crystalline limestone traversed by blackish veins running in a more or less nearly vertical direction. With these rocks the colours and markings of the snake harmonise in a remarkable manner, a blackish line along each side of the reptile's tail simulating the veins in the rock. Young specimens have not been found within the cave, and, if it really be that the species breeds only in the open, the resemblance in colouring must be due to fading in each individual. This snake is known as *Coluber tæniurus*. It has also been discovered that an allied member of the same genus—*C. moellendorffi*—takes up its quarters in a cavern in Tonkin. Although the cave is of limestone, the colouring of the snake is quite different from that of the Malay species, the upper parts being grey with dark spots and the tail ringed with red and black. Hence, it has been argued, the resemblance of the Malay species to its surroundings is accidental.

As occupying a somewhat intermediate position between the subject of haunts, or "station," and geographical distribution, reference may be made to the abundance of reptilian life in certain so-called "oceanic" islands where mammals are altogether unknown. The best instance of this is afforded by the islands of the Galapagos group, off the west coast of South America almost on the equator, which are tenanted by a number of giant land-tortoises of the genus *Testudo*, as well as by two large species of iguana, each representing a genus by itself (*Amblyrhynchus* and *Conolophus*). Giant land-tortoises also inhabited the Mascarene and the Seychelle islands till they were more or less completely exterminated by man.

It has been held that the Galapagos are truly oceanic islands, that is to say, they have been raised from the ocean without ever having formed part of a continent.

But Dr. J. Baur, who visited the islands in 1890, wrote as follows:—

"In this case there must have been a time when not a single organism existed on the islands. Only by accidental



A GIANT LAND-TORTOISE (*TESTUDO DAUDINOI*) OF SOUTH ALDABRA ISLAND



introduction from some other part of the earth could the islands be populated; but on such a supposition we are unable to explain the harmonious distribution, we cannot explain why every, or nearly every, island has its race or species. If some animals could be carried hundreds of miles to the islands, why are they not carried from one island to the other? But, besides this, how could we make plain the presence of such peculiar forms as the gigantic land-tortoises, for instance? According to the elevation theory, we can only think of an accidental importation of these tortoises by some current, because they are unable to swim. After the islands had been elevated out of the sea, it happened once, by a peculiar accident, that a land-tortoise was carried over. Alone it could not propagate.<sup>1</sup> This was only possible after a similar accident imported another specimen of the same species, of the opposite sex, to the same island. Or we could imagine that at the same time animals of both sexes were thus accidentally introduced. By this we could at least explain the population of a single island. But how did all the other islands become populated? To explain this we should have to invoke a thousand accidents.

"The most simple solution is given by the theory of subsidence. All the islands were formerly connected with each other, forming a single large island; subsidence kept on, and the single island was divided into several islands. Every island developed, in the course of long periods, its peculiar races, because the conditions on these different islands were not absolutely identical."

In other words, in place of being "oceanic," the Galapagos group is "continental," and was once joined to the American mainland. And there is little doubt that a similar explanation must hold good with the other "tortoise-islands". In Tertiary times giant tortoises of the genus *Testudo* inhabited all the great continents; the earliest known form being *T. ammon* of the Lower Eocene of Egypt, which may have been the parent stock of all. It is from these continental tortoises that the island forms of to-day are derived.

It may be mentioned that the great antiquity of giant tortoises of the genus *Testudo* affords an excellent example of the early date, as compared with mammals, of the dispersal

<sup>1</sup> Unless it happened to be a female with eggs (R.L.).

of reptiles, to which attention is more particularly directed in the paragraphs immediately following.

The subject of the distribution of reptilian life on the globe at the present day is so extensive and complex, and involves the consideration of such a number of problems, that to accord it anything like adequate treatment would demand the greater part of the space accorded in the present work to reptiles. Obviously, therefore, only the vaguest sketch can be attempted.

In the first place, it must be noted that, owing to the much greater antiquity of reptiles as a whole than mammals or birds, their dispersal, or "radiation," has taken place at a much earlier date than that of either of the latter groups. This, then, would be sufficient to demonstrate that the zoological "realms and regions" into which the surface of the globe has been parcelled out on the evidence of the present and past distribution of mammals and birds would not hold good for reptiles. This, however, is by no means all, for a study of the distribution of the existing orders of reptiles shows that there is little in common between them, and that each (doubtless owing to the different dates at which the groups have come into existence) has a "dispersal," or "radiation," of its own. Hence, not only cannot the distribution of reptiles be brought into line with that of mammals, but we cannot even map out a series of zoological regions for reptiles as a whole.

Certain facts in regard to the distribution of reptiles present problems which it is difficult to explain, in the present state of knowledge. Taking, for example, the northern hemisphere, of which the greater part is included in the Holarctic region of geographical zoology, with a Palæarctic, or Old World, and a Nearctic, or New World, subdivision, we find an extensive community of mammalian types, due to the fact that in post-glacial times there existed a circumpolar mammal fauna, the members of which passed by way of which is now Bering Strait from one hemisphere to the other. On the other hand, no such circumpolar reptilian fauna existed in comparatively modern times, for the reason that reptiles cannot withstand the rigours of Arctic cold, and consequently could not pass from one hemisphere to the other across Bering Strait, in the same manner as the elk and the wapiti reached Alaska from Asia. The difficulty in the case of the reptiles is exemplified by the alligators,

of which one species inhabits Eastern China and the other Eastern North America. This distribution seems at first sight to preclude the Bering Strait route, but the migration may have been earlier than that of the mammals, when the temperature was higher. At any rate, it is difficult to invoke the aid of land connections for modern types of reptiles which are not recognised in the case of mammals.

A remarkable feature in the distribution of reptiles is the community between the faunas of Madagascar and South America, as exemplified by certain snakes, iguanas, and fresh-water tortoises. In the case of the tortoises the genus *Podocnemis* is common to those two widely sundered areas, and the same community of generic type holds good for certain snakes. In the case of the tortoises it is possible to explain this remarkable distribution by supposing that different members of the genera in question travelled down the continents bordering the two sides of the Atlantic, as extinct members of the group are found fossil in the Eocene Tertiary rocks of the northern hemisphere. On the other hand, certain extinct tortoises (*Miolania*), of which no representatives are known in the northern hemisphere, occur respectively in Queensland and Patagonia. Their distribution it seems possible to explain only by a connection of the southern continents and islands in a southern zone; and this being so, it is difficult to deny that the Malagasy and South American species of *Podocnemis* have not travelled by the same route;—a route which may perhaps best explain the distribution of the snakes and iguanas, despite the fact that representatives of the latter are met with in a fossil state in the European Tertiaries. It should be added that certain genera of tortoises, such as *Pelomedusa* and *Sternotherus*, are peculiar to Madagascar and Africa, thus bringing, with the help of the aforesaid *Podocnemis*, the fauna of the latter continent into connection with that of South America, and so with Australia.

Such are a few of the puzzling problems presented by the distribution of reptiles; but to dilate further on this subject is impracticable, and I accordingly pass on to glance at some of the leading features in the distribution of the more important groups of reptiles.

As regards the Chelonia, of which the northern range in

the western hemisphere is limited by latitude  $50^{\circ}$  and in the eastern by latitude  $56^{\circ}$ , the most remarkable feature is the limitation of the pleurodiran group (in which the neck is retracted by a horizontal flexure) to the southern hemisphere, where they occur in all the three continents, and in Australasia to the exclusion of the cryptodiran group (in which the neck is retracted by an S-like flexure in a vertical plane). Of the two chief families of Pleurodira, the *Pelomedusidæ* are common to Africa, Madagascar, and South America, while the *Chelyidæ* occur in South America and Australasia (exclusive of New Zealand), although there is no generic type common to the two areas. As regards the Trionychoidea, or soft river-tortoises, the group is confined to Africa, Tropical Asia, and Eastern North America, to the exclusion of South America and Australasia; the distribution in America and Asia being thus comparable to that of alligators, although more extensive in the latter area. Of the terrestrial and fluviatile families of the Cryptodira, the snappers, *Chelydridæ*, are American, ranging as far south as Ecuador, but are represented in the Miocene of Europe. The *Dermatemydidæ* and *Cinosternidæ* are North and Central American; the *Platysternidæ* are confined to Eastern Asia, and the *Testudinidæ*, especially as represented by the typical land-tortoises of the genus *Testudo*, are cosmopolitan, with the exception of being unknown in the Australasian area.

The Crocodilia are found in the warmer regions of all the great continents, inclusive of Northern Australia, as well as in the larger tropical islands. Crocodiles (*Crocodilus*) in the New World are confined to Central America and the northern extremity of South America, but elsewhere their distribution is coextensive with that of the order. The distribution of true alligators (*Alligator*) has been already referred to; but caimans or South American alligators (*Caiman*) are natives of Central and South America. On the other hand, the long-snouted gharials (*Gavialis* and *Tomistoma*) are restricted to India and the Malay countries.

The Rhynchocephalia are confined at the present day to New Zealand, whose only other reptiles are geckos and skinks.

Chamæleons are an essentially African and Malagasy group, with outlying forms in the south of India and Arabia and in

Ceylon, and also known (although perhaps introduced) in the south of Spain. Madagascar appears to be the headquarters of the group. The geckos (*Geckonidæ*, etc.) are practically cosmopolitan, exclusive of the colder regions of the globe. Another cosmopolitan family is that of the skinks (*Scincidæ*) whose headquarters are Australasia, with representatives in New Zealand.<sup>1</sup> The stellions (*Agamidæ*), monitors (*Varanidæ*) and typical lizards (*Lacertidæ*) are confined to the eastern hemisphere; the latter having, however, a much more restricted range than the other two, not entering the Australasian region, and being likewise unknown in Madagascar. The latter island and New Zealand have no stellions or monitors, which are otherwise distributed over the greater part of the warmer zones of the eastern hemisphere.

On the other hand, the iguanas (*Iguanidæ*) form an essentially American group, which attains its maximum development in the tropical districts; but it has three outlying generic types, two of which occur in Madagascar, and the third in the Fiji and Friendly Islands.<sup>2</sup> Extinct forms, as already mentioned, are known from the European Tertiaries. The amphisbænas (*Amphisbænidæ*) have a wider range, occurring in America, the West Indies, Africa (but not Madagascar), and the Mediterranean countries; a very puzzling distribution, which is in no wise rendered more easy of explanation by the suggestion that these burrowing lizards are related to the tropical American family of tejus (*Teiidæ*). Finally, the slow-worms (*Anguidæ*) are distributed over Europe, Northern Africa, Northern India, and the warmer parts of America; while their less specialised relatives the girdle-tailed lizards (*Zonuridæ*) take their place in Africa south of the Sahara and Madagascar.

Apart from the tuatara of New Zealand, Australasia is seen to be inhabited only by geckos, skinks, stellions, and monitors; and thus exhibits none of that marked relationship to South

<sup>1</sup> In the volume on reptiles in the *Cambridge Natural History* it is stated (p. 500) that there are no skinks in New Zealand. There are, however, for example, two species of *Lygosoma* (see *Cat. Rept. Brit. Mus.* iii., pp. 271 and 272).

<sup>2</sup> In the work cited in the last note it is suggested that these eastern iguanas are not *Iguanidæ* at all, but have attained a resemblance to that family by "convergence". If resort be had to such an explanation in all cases of difficulty, it would tend to show that our present schemes of classification are practically valueless.

America displayed by its tortoises, or indeed to Madagascar. This latter island, on the other hand, lacks stellions, monitors, typical lizards, slow-worms, and amphisbænas, while it possesses, in addition to the cosmopolitan skinks and geckos (of which latter there are some very peculiar types) chamaeleons and the African families *Zonuridæ* and *Gerrhosauridæ*.

Lizards have the most northerly range of all reptiles, extending in British Columbia to about latitude 56° and in the Old World almost to the Arctic circle. In the southern hemisphere they extend to the extremity of the American continent.

Snakes, on the other hand, stop considerably short of the above limits, both in the north and in the south. The sub-order is practically cosmopolitan, New Zealand being the only large island (other than those of the polar regions) in which it is wanting. Nor is this all, for dangerously poisonous species are to be met with throughout the distributional area of the group with the exception of Madagascar,<sup>1</sup> which enjoys complete freedom from such noxious creatures. A great contrast in this respect is presented by the Oriental region of geographical zoology (India, the Malay countries, and southern China), which is the home of members of the three most important groups of poisonous serpents, and has consequently the highest death-rate from snake-bite of any part of the world.

The four families of burrowing snakes, namely *Typhlopidae*, *Glauconiidæ*, *Ilysiidæ*, and *Uropeltidæ*, appear to indicate an ancient type, since some of them retain traces of the hind limbs, and it is therefore not surprising to find that, as a whole, they have a wide geographical range, although the last of the four is restricted to Southern India and Ceylon. The boas and pythons (*Pythonidae*), again, which likewise appear to be a comparatively ancient group, have also a wide range in space, being almost cosmopolitan. Of the two subfamilies into which the group is divided, the pythons (*Pythoninae*) are almost exclusively Old World types, large species of the typical genus occurring in Africa, India, the Malay countries, etc., and smaller forms in Australia. The one exception to the Old World distribution of this subfamily is the occurrence of *Loxocemus bicolor* (the

<sup>1</sup> Ireland has, of course, the same immunity, but it can scarcely be recognised as a large island.

sole representative of its genus) in Southern Mexico. On the other hand the boas (*Boinae*) are mainly characteristic of tropical America, the home of the gigantic anaconda. There are, indeed, certain Old World generic types (*Eryx*, *Enygrus*, and *Casarea*), but the remarkable feature in the distribution of the family is the occurrence of representatives of the American genera *Boa* and *Corallus* in Madagascar;—a peculiarity paralleled by the distribution of *Podocnemis* among the tortoises.

As regards the distribution of the family *Colubridæ*, which includes the majority of snakes, a brief notice must suffice, as many of the groups have a cosmopolitan range. Considerable interest attaches, to the distribution of the poisonous sub-family *Elapinæ* (which includes the cobras of India and Africa). This group ranges over the tropical and sub-tropical regions of both hemispheres (exclusive of Madagascar), but is particularly characteristic of Australia, where other snakes are represented only by a few pythons and blind snakes (*Typhlopidae*) and a small number of *Colubrinæ*, or typical snakes. Nearly allied to the *Elapinæ* are the sea-snakes (*Hydrophiinæ*), which range from the Persian Gulf to Central America. Noteworthy, too, is the distribution of the *Amblycephalidæ*, a small family of snakes allied to the *Colubridæ*, of which some forms are found in tropical America and the rest in the Oriental region.

The vipers (*Viperidæ*) have a nearly cosmopolitan distribution, although absent from Madagascar and Australia; but whereas true vipers (subfamily *Viperinæ*) form an exclusively Old World group, pit-vipers (*Crotalinæ*) are represented in tropical Asia as well as in both North and South America. In this subfamily the rattlesnakes (*Crotalus*) form a characteristic and widely distributed American group, although they have near relatives in the Old World, which are however unprovided with the distinctive rattle.

As is evident from the statement already made as to their absence from the high north, reptiles are extremely sensitive to cold; and in temperate climates the whole of the species hibernate for a longer or shorter period in the cold season. With the exception of those adapted to a life in the desert, reptiles, and especially the sub-aquatic kinds, are intolerant of intense dry heat, and certain kinds “æstivate,” or become torpid, during such periods.

A few words may be devoted to some of the features of desert reptiles—a subject which has been studied by Dr. Boettger, in the steppes of Transcaspia. In that district the winter, although comparatively short, is of great severity, while the summer is remarkable for its intense heat. The advent of spring clothes the ground with a carpet of lilies, tulips, and other flowers; but their season is short, the heat of summer and the autumnal sandstorms reducing the country to a desert. The scattered vegetation has mostly narrow, or even needle-like leaves; and the sand-heaps round the root of each plant form harbours for the lizards and snakes, the limited number of species of which abound in individuals. Among the most characteristic desert types are various skinks, such as *Chalcides* and *Teratosaurus*, certain geckos which have forsaken the normal habitats of the group for this kind of existence, species of *Phrynocephalus* among the *Agamidæ*, four members of the family *Lacertidæ*, and *Varanus griseus* representing the monitors. Neither are snakes wanting, the harmless kinds being represented by about half a score of species, among which the sand-burrowing *Eryx jaculus* is a well-known type; while the venomous sorts include the asp or cobra, and the sand-viper (*Echis arenicola*). Most of these reptiles are sandy brown in colour, marked with dark spots or stripes; and many of them exhibit other adaptations. The lizards and snakes are, for instance, markedly elongated, while the latter have an unusually large number of horny shields on the lower surface of the body. Some have the muzzle specially shaped for digging in the burning sand; and in others the scales are so arranged as to retain the sand when heaped up on the back. In most of the snakes the nostrils are protected by valves, or much reduced in size; but in the burrowing species they are situated on the top instead of in the front of the snout. The ears are also protected in a similar manner. Most remarkable of all these adaptations is the presence of a "window" in the lower eyelid of the skinks of the genera *Mabuia* and *Ablepharus*; the two eyelids being fused together in the latter. A similar arrangement obtains in certain typical lizards. None of these desert reptiles aestivates.

Crocodiles and alligators may be cited as examples of reptiles that aestivate when their haunts are desiccated; burying

themselves at such times deep down in the mud, where they remain till the return of moisture. Writing of the South American alligators, or caimans, the late Mr. H. W. Bates observes that: "Like the turtles (*Podocnemis*), the alligator has its annual migrations, for it retreats to the interior pools and flooded forests in the wet season and descends to the main river in the dry season. During the months of high water, therefore, scarcely a single individual is to be seen in the main river. In the middle part of the Lower Amazons, where many of the lakes with their communicating channels dry up in the fine months, the alligator buries itself in the mud and becomes dormant, sleeping till the rainy season returns. On the Upper Amazons, where the dry season is never excessive, it has not this habit, but is lively all the year round."

In the preceding paragraphs it has been mentioned that caimans and the great Amazonian tortoises make seasonal migrations. Similar migrations are undertaken by the European pond-tortoise (*Emys orbicularis*) when its haunts are dried up. Whether under such circumstances it will aestivate, I have no information. Another instance of seasonal migration among reptiles is afforded by the giant tortoises of the Galapagos Islands, which in the dry season make journeys into the interior in search of water. It does not appear, however, that any reptiles migrate south in winter in search of a warmer temperature: in fact their rate of progress would prevent such marches.

On the other hand, as already stated, all reptiles inhabiting cold climates hibernate. The pond-tortoise, for example, buries itself in mud in autumn, and does not reappear till the spring is well advanced; while some of the American terrapins burrow in the banks for their winter slumber. As is well-known, the South European land-tortoises kept as pets in England retire for the winter months; but in their native countries the period of torpor must be less prolonged. Here it may be mentioned that no reptile can stand being frozen; so that if they do not burrow deep enough, such hibernating tortoises are likely to perish in severe winters.

British snakes and lizards undergo a long hibernation, retiring in autumn, and not reappearing till spring. In the case of the grass-snake it is not unusual for several individuals to occupy

the same hole ; and occasionally a number of individuals have been found coiled up into a solid mass. The most extraordinary instance of such a collection of these snakes (which were not hibernating) was recorded a few years ago in the month of September near Llanelly, South Wales, where they took possession of a house. The reptiles crawled over the floors, infested the cupboards, curled themselves together on the furniture, while some individuals climbed the stairs and luxuriated in the comforts of the bedrooms. The human occupants of the house had done their best to rid themselves of these unwelcome visitors, and had waged a war of extermination against them. The snakes continued to come, however, although no fewer than twenty-two were slaughtered in one day. The eggs from which the twenty-two individuals were hatched were probably deposited by the parent behind the oven, or in a hole in the back wall. On taking down a portion of the latter wall forty bunches, each containing thirty eggs, were discovered, all on the point of hatching. There were thus some twelve hundred snakes in an area of a few square feet.

Similar large congregations of rattlesnakes are well-known in certain parts of North America about the commencement of the hibernating season. In some districts it is reported that the snakes used to collect in hundreds, or even thousands, in the den, to which they travelled from distances of thirty or forty miles. Whether all reptiles that hibernate fatten themselves preparatory for their fast, does not appear to be ascertained. It is stated, however, that chamæleons certainly do so ; and that in North Africa at any rate they retire for the winter under ground, although how long they remain there is unknown. It is likewise not ascertained whether any of the tropical species æstivate.

## CHAPTER IV

### FOOD AND GROWTH

Food. Mode of killing prey. Snake-eating snakes; egg-eating snakes. Fascination. Rate of growth. Age. Vitality. Regeneration. Chronic disease. Sloughing of skin. Peculiar associations.

THE food of reptiles is very various ; and while in some groups the nature of the diet is more or less similar in all the species, in other cases there is a remarkable diversity in this respect among closely allied forms. Crocodiles are typically carnivorous reptiles, tearing the carcases of the animals on which they subsist with their powerful and sharp-pointed teeth before devouring them. From the nature of their teeth we may also infer that the typical dinosaurs, such as *Megalosaurus*, as well as the theriodonts, belodonts (*Phytosaurus*), ichthyosaurs, and plesiosaurs, were likewise carnivorous ; the food of the last two groups probably consisting of the contemporary mail-clad fishes. Such of the pterodactyles as were furnished with teeth were likewise in all probability to a great extent, if not altogether, fish-eaters. And if this be so, we can scarcely refuse to believe that their toothless brethren, in which the jaws were probably sheathed with horn, subsisted on similar food. At first sight, indeed, it may seem strange that this marked difference in the armature of the jaws does not imply a corresponding difference in the food ; but the case of the chelonians, in which a toothless horny beak is correlated in some instances with a carnivorous, and in others with a herbivorous diet, seems to negative this idea. For example, while the common green turtle (*Chelone mydas*) is herbivorous, the closely allied hawksbill (*C. imbricata*) is strictly carnivorous, feeding upon fishes and molluscs. Again while the land-tortoises (*Testudo*) are purely vegetable feeders, the common pond-tortoise (*Emys orbicularis*) and some of its near relatives are carnivorous, subsisting on fishes, molluscs, worms, insects, etc. On the other hand,

the large batagurs (*Batagur*, *Cachuga*, etc.) of the Indian rivers are as purely herbivorous. Indeed the only group of chelonians which is constant in the matter of diet appears to be the soft river-tortoises (*Trionychidæ*), which are wholly carnivorous.

Snakes of all kinds subsist on an animal diet, which may, however, consist of the entire bodies of land-animals, swallowed whole, of eggs, of fishes, or in the case of the burrowing species, of worms and other subterranean creatures. The pythons and boa-constrictors crush the bodies of the animals they have seized for food within their lithe coils until the former are reduced to the condition of a sausage, when, after being lubricated with saliva, they are swallowed whole. Exaggerated stories are undoubtedly current as to the size of the animals a five-and-twenty-foot python is capable of gorging ; but we have no definite means of gauging the capacity of these voracious reptiles in this respect. The fibrous (instead of bony) union between the two branches of the lower jaw in all snakes is a special adaptation for the swallowing of such huge boluses. After a gorge of this nature a python, like other large snakes, requires a long period of quiescence, which is passed in a kind of semi-torpor, before it is ready for another meal.

The following particulars in regard to the amount of food consumed during one year by snakes in captivity were published in the report of the Trivandrum Museum, Travancore, for 1903 ; the dates when the reptiles changed their skins being likewise given :—

A Malay python 21 ft. long, ate 100 fowls, two hare-wallabies, two bandicoots, one kangaroo, and one dog. It shed its skin on 30th September, 11th December, 1902, and 18th February, 12th April, and 9th June, 1903. An Indian python measuring 15 $\frac{1}{4}$  ft. in length, ate fifty-four fowls, two bandicoots, two dogs, two guinea-pigs, one heron, and two hare-wallabies. Its skin was shed on 22nd August, 9th October, 17th December, 1902, and 6th February, 1st April, and 2nd June, 1903. Another example of *Python molurus*, 8 $\frac{1}{2}$  ft. long, ate during the year nineteen fowls, four bandicoots, and one dove ; shedding its skin on 14th September, 26th December, 1902, and on 19th February, 8th April, and 19th June, 1903. Yet another, 9 ft. long, ate fifteen fowls, one bandicoot, and one hare-wallaby. This snake

shed its skin on 20th August, 15th October, 1902, and on 13th January, 16th March, 1903. A king-cobra, length  $8\frac{1}{2}$  ft., ate during the year forty-four rat-snakes, shedding its skin on 7th October, 25th December, 1902, 19th February, 29th April, and 17th July, 1903. A cobra (*Naia tripudians*),  $5\frac{1}{4}$  ft. long, ate fifty-five rats and fifty frogs. It shed its skin on 10th November, 1902, and 19th February, 8th April, and 28th July, 1903. A Russell's viper consumed fifty rats in the year, shedding its skin on 24th September, 26th December, 1902, and 17th April, 1903. Finally, a rock-snake ate during the year sixty-seven frogs. It shed its skin on 13th February, 20th April, 13th June, and 12th August, 1903.

As already stated, the king-cobra of South-Eastern Asia, which reaches a length of 15 ft., is in the habit of preying on non-venomous serpents of other species. A specimen of this snake measuring a little over 11 ft. has been seen in Burma carrying another member of its own species in its jaws, while on a second occasion a king-cobra was observed in the act of eating an ordinary cobra, and in a third case a cobra had been swallowed. Another king-cobra has been known to devour a banded krait; while from the stomach of yet another specimen was taken the still more venomous Russell's viper. At first sight these instances suggest that the devourer must be immune to the venom of the devoured; but such conclusions are not justified by the present state of information with regard to the action of serpent-poison.

In captivity a python has been known to devour one of its own kind, and likewise the blanket with which it was supplied as a protection against cold; although both these instances were probably due to the depraved habits so often developed among animals in captivity. But the snake-eating, or king, cobra, takes its name from its habit of preying on other snakes, especially the rat-snake, which also derives its name from the nature of its diet.

Many snakes apparently devour the eggs of birds and other reptiles when opportunity occurs; and when the snake is large and the egg small, there need not necessarily be any special difficulty in thefeat. The difficulty comes when the snake is small and the egg large. A special adaptation enables, however, the egg-eating snake (*Dasypeltis scabra*) to accom-

plish this feat without undue difficulty. This reptile, a native of South and Tropical Africa, and less than a yard in length, is able to swallow a hen's egg, while specimens a foot in length will "get outside" a pigeon's egg. The means by which this is accomplished are simple and ingenious. The lower spines of some of the vertebræ are so lengthened as to pierce the upper side of the gullet, on the surface of which they appear as small teeth-like knobs ; and when an egg is swallowed it is crushed or sawn through by these projections. After the egg, with some difficulty, is swallowed (the skin of the snake being dis-



FIG. 3.—African Egg-eating Snake and its mode of swallowing food.

tended almost to bursting), it gradually glides further and further down till it comes to the projections in the gullet, when the swollen part of the snake's neck suddenly resumes its normal size ; and, after an interval, the broken shell is disgorged. A similar structural peculiarity characterises an Indian snake belonging to a different group, and known as *Elachistodon westermanni* ; from which it has been suggested that this species also displays egg-swallowing propensities. If the suggestion be well-founded, we shall have an instance of the independent development in two groups of an adaptation to the same end.

Monitor lizards (*Varanus*) are likewise consumers of eggs,





HEAD OF AFRICAN PUFF-ADDER (*BITIS ARIETANS*), SHOWING  
POISON-FANGS



POISONOUS LIZARD (*HELODERMA SUSPECTUM*) OF ARIZONA

but since these reptiles are large, they have no difficulty in regard to swallowing such delicacies, which are taken into the mouth, when, with the head held well up, the shell is cracked and the contents allowed to flow down the throat. A Bengal monitor (*V. bengalensis*) kept in the gardens of the Trivandrum Museum devoured in the course of a twelvemonth sixty rats, 10 lb. of beef, six eggs, and four guinea-pigs. Skinks form a large portion of the food of monitors in some districts.

All chamæleons are insectivorous, and the same is the case with a number of true lizards, such as the stellions (*Agama*) and the typical lizards (*Lacerta*). Many lizards, however, such as the stump-tailed skink (*Trachysaurus*), subsist on a mixed diet; but, judging from the nature of their teeth, the large Australian skinks of the genus *Tiliqua* are probably herbivorous. The American iguanas exhibit that diversity of diet in different groups already mentioned as a curious feature among reptiles. For instance, whereas the anolis iguanas of the genus *Anolis* are insectivorous, the true iguanas (*Iguana*), the basilisks (*Basiliscus*), and the Galapagos iguanas (*Conolophus* and *Amblyrhynchus*) are herbivorous. The last-mentioned, or sea-iguana, is peculiar among the group in feeding on sea-weeds.

A superficial resemblance in the teeth of the dinosaur of the Wealden to those of the iguanas suggested to Dr. Gideon Mantell, its describer, the name of *Iguanodon* for the former; and it would appear that this resemblance is correlated with the nature of the food in the two groups, for the iguanodons, as proved by the manner in which their teeth became worn down, were certainly herbivorous. Another group of dinosaurs, with teeth of a somewhat similar type, as exemplified by the European *Pelorosaurus* and *Hoplosaurus* and the American *Brontosaurus* (*Apatosaurus*) and *Diplodocus*, are likewise generally considered to have been herbivorous. In 1910 Mr. J. Versluy's suggested, however, that *Diplodocus* and its kin subsisted on fishes. In support of this it is pointed out that the capacity of the body-cavity is not large enough to have contained a sufficient supply of vegetable food. Moreover, it is argued that the length and mobility of the neck, coupled with its muscular power (as demonstrated by the prominences on the bones), and the small size of the head, apparently indicate rapid and definite

movements in water. Then, again, the nature of the dentition and the form of the mouth-cavity appear adapted for a fish-diet. And it is accordingly suggested that these huge reptiles captured fishes near the borders of lakes and rivers, which they swallowed whole without mastication. The number of representatives of the Chelonia which are vegetable-feeders has been already referred to, but it may be mentioned that the giant land-tortoises of the Galapagos, together with the land-iguana of the same islands, subsist on large cactuses, which form the chief vegetation of those islands.

Lastly, the New Zealand tuatera (*Sphenodon*), the sole existing representative of the Rhynchocephalia, subsists upon animal food, although the nature of this seems to vary according to individual taste. Some specimens, for instance, consume insects and worms, and those which frequent the shore not improbably eat crustaceans. This suggests that the food of the extinct Triassic pavement-toothed tuatera (*Hyperodapedon*) may also have consisted of crustaceans and perhaps of molluscs. The bean-toothed reptiles (Placodontia) almost certainly subsisted on a diet of the latter type.

Brief reference to certain peculiar modes in which some reptiles capture or kill their prey must suffice. An ingenious method of capturing flies and other insects is employed by chamæleons, in which the tongue is developed into an elastic, trumpet-like organ which can be shot out to a long distance in front of the mouth, and is furnished at its tip with a glutinous secretion for securing the prey. Crocodiles and alligators, having seized their victims in their cruel jaws, hold them under water until they are drowned; and it would seem that these reptiles have developed the peculiar respiratory mechanism by means of which they are enabled to breathe while their mouths are under water for this purpose. Pythons kill their victims by encircling them in their coils and gradually crushing the life out of them; and vipers and other venomous snakes kill their prey by injecting poison into their tissues. In this connection it is interesting to notice that the poison of different groups of snakes is designed to destroy with the greatest rapidity the particular kinds of animal on which they severally prey. The venom of the sea-snakes, for example, acts much more powerfully on fishes than on land animals, while that of cobras

and vipers exerts its deadly effect with the greatest rapidity on mammals and birds. Here it may be noted that certain animals, such as the ichneumon and the hedgehog, appear to be immune to snake-poison..

There is an ancient belief that snakes possess the power of "fascinating," or, in other words, inducing a kind of paralysis in the animals upon which they are about to prey. For many years this idea has, however, been discredited by naturalists, and it may be said to have received its deathblow as the result of observations conducted in the menagerie of the Zoological Society of London, of which an account will be found in the Society's *Proceedings* for 1908.

According to these observations, it appears that in the majority of such supposed cases of fascination there is not the remotest pretext for believing in the existence of any such power. Many animals, however, are of an inquisitive disposition; and in the case of the smaller mammals and birds, this is associated with the power of attention. If a movement be sudden or noisy, they start off at once; but if it be slow, silent, and stealthy, they remain motionless, although intensely watchful. If a snake be prompt in seizing that moment of watchfulness, it may secure its prey, but a human hand slowly advanced has just as much power of fascination.

These observations likewise demonstrate that, except in the case of one particular group, animals display no special fear of snakes; the majority of species, such as frogs, rats, mice, guinea-pigs, rabbits, ruminants, and birds, being absolutely indifferent to the proximity of a serpent—venomous or otherwise; and even when the latter approaches them, avoid it as they would a stick when thrust in their direction. On the other hand, apes and monkeys—but not lemurs—display a marked instinctive dread and recognition of snakes. This is displayed whether the reptiles are venomous or harmless.

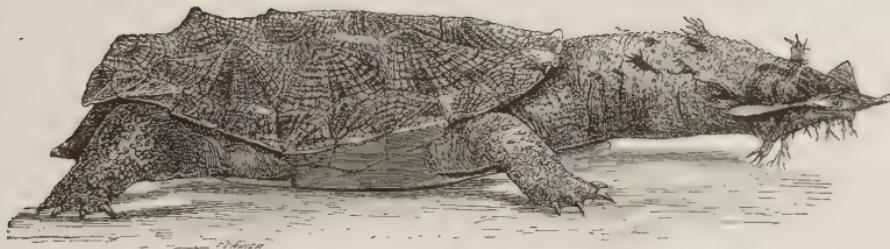
When the recorders of these observations approached the cages in the monkey-house with a group of writhing snakes, "the monkeys at once fell back shrieking, whilst the lemurs crowded to the front of the cage, displaying the greatest interest and not the smallest perturbation when a snake was brought so close to them that its tongue almost touched their faces. We got the impression that had the lemurs been given the

opportunity, they would at once have seized and tried to devour the snake. The South American monkeys showed fear in irregular and sometimes slightly marked form. Spider-monkeys were quite as excited and alarmed as any Old World monkey. Some of the larger *Cebidæ* did not retreat, but uncovered their canines, and looked as if they were ready to show fight. The Old World monkeys recognised the snakes instantly and bolted panic-stricken, chattering loudly and retreating to their boxes or as high up as possible in the larger cages."

The writers conclude that in all probability "human beings have inherited this specific fear of snakes from their anthropoid ancestors, and that our inclination to attribute a similar fear of snakes to other animals is due not merely to erroneous observation but to an 'anthropoidomorphic' prepossession".

A remarkable provision for the purpose of attracting prey within reach occurs in the mata-mata terrapin (*Chelys fimbriata*) of Brazil and the Guianas. In this reptile the head and neck are fringed with warty appendages, floating in the water like some vegetable growth, whilst the rough, bossed carapace resembles a stone,—an appearance which evidently is of as great use to this creature in escaping the observation of its enemies as in alluring to it unsuspecting animals on which it feeds. It would seem that in this chelonian we have a double adaptation;—one for attracting prey, and the other to harmonise with the surroundings.

As mentioned in the first chapter, no reptile undergoes a metainorphosis, or transformation, comparable to that of amphibians, so that the life-history of all the members of the group is comparatively simple, consisting in the main of a gradual and regular increase in size from birth to maturity. It is true, that the young of some reptiles are more brightly coloured than their parents, while the newly-born offspring of crocodiles are furnished with an "egg-tooth". These, however, are but trifling points of difference; and, in many cases at any rate, no one would have much difficulty in declaring the specific identity of a young reptile with its parent. A young gharial, for example, of half a dozen inches in length, is a miniature of its parents, with the exception that if it be a male, it lacks the protuberance at the extremity of the muzzle characteristic of adult males.



THE MATA-MATA TERRAPIN (*CHELYS FIMBRIATA*)



NILE SOFT-TORTOISE (*TRIONYX TRIUNGUIS*)



The uniform growth distinctive of reptiles may apparently cease only with the extinction of life; and for this reason it seems unwise to discredit the stories of unusually gigantic crocodiles, pythons, and anacondas which are from time to time reported, although in some cases these are doubtless exaggerated.

An idea is prevalent that the growth of reptiles is exceedingly slow, and this is doubtless true in many cases. For instance, the young of the scheltopusik, or glass-snake, are stated to be many years in coming to maturity. It is also practically certain that the giant land-tortoises of the Mascarene and Galapagos Islands take an immense time before reaching their full size. Again, the American painted terrapin is known, from the result of observation, to be very slow in its growth. A specimen, for instance, in which in its second year the shell measured 26·5 millimetres in length, took twenty-five years before it attained a full average shell-length, that is to say 121 millimetres; and it is inferred that an example in which the shell measured 163 millimetres was much older. That the rate of growth of the first specimen was normal, is demonstrated by the circumstances that for many years it progressed *pari passu* with that of a number of other examples kept under observation. These showed that during the first half-dozen years the rate of increase is so regular that specimens can be arranged in series corresponding to their age from their similarity in size. Up to this period the age of specimens is indicated by the number of lines of growth on the horny shields covering the shell; but after the seventh year these shields tend to become smooth so that the annual lines of growth become more or less obliterated, when the possibility of reckoning the age by this means becomes proportionately difficult.

On the other hand, statements as to the slowness of growth of the American alligator (*Alligator mississippiensis*) are not supported by observations on specimens in the New York Zoological Park. It was stated, for instance, by an American writer that: "Alligators grow very slowly. At fifteen years of age they are only two feet long. A twelve-footer may be reasonably supposed to be seventy-five years of age."

The observations at the New York Zoological Park showed that young alligators when first hatched measured eight inches

in length; while when a year old their length was eighteen inches, showing an increase of ten inches in a twelvemonth. A year later (in August) their average length was twenty-three inches; but in the following March their average length was three feet nine inches. At the time when these last measurements were taken the alligators were only two and a half years old, during which time they had increased thirty-seven inches in length. Probably the rate of growth would not continue at this rapid pace, but even so an alligator of twelve feet in length need not be more than a dozen years old.

It might be urged that the growth of specimens in captivity is abnormally rapid; but even if this were so, the rate in a wild state would be in excess of that given in the passage quoted above. The observer who recorded the dimensions of the New York specimens is, however, of opinion that the growth in the wild state is at least as rapid as in the case of captive specimens<sup>1</sup> :—

“ From observations made in the South Carolina bayous by the writer, it would seem that the growth of wild alligators must be fully as rapid if not more so, than that of the specimens reared in captivity. The females construct their nests near shallows teeming with fish, and in an atmosphere of heat and humidity. The young reptiles probably grow more rapidly when wild than when confined. Of course hibernation must be considered in the case of the wild reptile. During this period growth must be very slow, or cease altogether. Yet the writer has always noted that reptiles in captivity, no matter how elaborate may be the facilities for their care, or the voracity evinced by the reptiles themselves, never grow so rapidly as those in a wild state. Repeatedly has this been observed by comparing the young of wild and captive-bred snakes, the ages of which are easily distinguished.”

As to the duration of life in reptiles, information is imperfect, although the most satisfactory dates are afforded among tortoises, some of which attain an age which may be counted by centuries instead of years. As we have seen, the painted terrapin is known to live more than five-and-twenty years. Again Gilbert White's tortoise “Timothy,” which belonged to the species *Testudo ibera* and whose shell is exhibited in the

<sup>1</sup> Seventh Annual Report, New York Zoological Society, p. 150.

reptile gallery at the British Museum, is known to have lived fifty-four years at the date of its decease in 1794 ; but how much has to be added to this is uncertain, since there is no clue as to its age when it was brought to England. Some idea as regards the age attained by giant land-tortoises is afforded by certain specimens from the Seychelles. In the year 1766 five tortoises belonging to the species *Testudo sumeirei* were taken from their island by the Chevalier Marion de Fresne and carried to Mauritius, where two were living a few years ago. The most celebrated of the pair is the one at the Artillery Barracks, Port Louis, of which the shell measures about forty inches in length in a straight line. Since the dimensions of the shell are reported to have been practically as large so long ago as the year 1810, it is certain that this tortoise must have been very old at the time of its arrival in Port Louis ; and something over a century would probably be a moderate estimate of its age at that date. Accordingly, it would seem that the reptile cannot be much less than 250 years, and may be much more.

Another aged specimen was the Colombo tortoise. According to tradition, this patriarch, which died in 1894, was found in Colombo when Ceylon was taken over by the British in 1796 ; having been imported from one of the "tortoise-islands".<sup>1</sup> At that time it was doubtless an unusually large and old specimen, or it would not have been kept, and we may accordingly allow it a minimum age of a couple of centuries. In a third case, that of the Egmont Island tortoise, the evidence as to the duration of its captivity is less satisfactory. It is reported to have lived on Egmont Island for a century and a half, but since the Chagos group (to which that island pertains) was not colonised from Mauritius till the early part of the nineteenth century, there is some doubt with regard to the statement. Nevertheless, it is certain that this monster must be of prodigious age. This tortoise was in the habit of burying itself and remaining dormant for half the year. Although nothing definite appears to be known with regard to other reptiles, there seems to be little doubt that crocodiles attain a great age ; and many years ago when Professor A. Leith-Adams visited the celebrated "magar-pit," or crocodile-pond, near Karachi, he was told that a large specimen of the Indian magar (*Crocodilus palustris*) was

<sup>1</sup> See Pearson, *Spolia Zeylanica*, vol. xxvi., p. 108, 1910.

supposed to be about two hundred years old, but this can only be taken as a general statement to the effect that it was of great age.

As might be expected from their cold blood and low organisation, reptiles display great vitality and power of recuperation from injury, although, as already mentioned, they will not stand being frozen. The most striking instances of this vitality are recorded in the case of the turtles, in which the heart will continue to beat for several hours after it has been removed from the body, while the flesh may be cut piece-meal from the body till little more than the skeleton remains before life becomes extinct. According to Sir J. Emerson Tennent, it was the custom in his time in Ceylon to cut pieces from the flesh of living turtles and sell them to customers as required. Again, as is mentioned elsewhere, it was the practice of the natives of the Galapagos Islands to cut a slit near the tail of the giant tortoises so as to reveal the interior of the body, and thus permit of ascertaining whether the reptile was sufficiently fat to be worth killing. If its condition was not found to be satisfactory in this respect, it was let loose, when it recovered without difficulty from the operation.

Closely connected with their vitality is the power possessed by many or most reptiles of regenerating lost parts. The most familiar and striking example of this power is afforded by the ease with which many lizards grow a new tail, or part of a tail, after having discarded a large portion of this appendage as a protective measure. Since this phenomenon is described in a later chapter, it need not be alluded to further on this occasion ; but it may be added that the power of discarding the tail and growing a new one is also exhibited by the New Zealand tuatara.

As regards chelonians, Sir J. E. Tennent states that in Ceylon when the horny plates are stripped off the hawksbill turtle (*Chelone imbricata*), after roasting the reptile over a fire, they are regenerated after the creature has been returned to the sea. It is affirmed in proof of this that no turtles are caught in a mutilated condition, but this, if the original statement be true, may be due to the circumstance that their sufferings are ended by death. On the other hand, Dr. Charles Hose states that turtles are caught in Borneo showing signs of having lost their horny plates, which have been replaced by thin and imperfectly grown ones of no commercial value.

That tortoises and turtles can regenerate their horny plates to some extent, provided the deep-seated, or malpighian, layer of the underlying skin be not destroyed, is, however, amply demonstrated. On this subject Dr. H. Gadow writes as follows in the volume on reptiles in the *Cambridge Natural History* :—

" If part of the horny covering is badly bruised, torn off, or rubbed through, or if part of the shell is crushed, the underlying portion of the horny plates becomes necrotic, and the horny covering also dies so far as its malpighian layer is destroyed. Soon, however, the uninjured malpighian cells, around the margin of the wound, multiply, grow into and beneath the injured portion of the bone, and form a new horny layer, casting off the necrotic portion. After several months the deficiency is patched up; new bone has grown in the deeper remaining strata of the cutis, and the outside is covered by a continuous horny layer, without, however, reproducing the original concentric moulding of the shields. In badly crushed shells sometimes almost one-third of the whole shell is thus cast off and mended within one or two years."

Should terrapins, as not infrequently happens, lose their tails or limbs by a bite, the missing part is never reproduced; the stump being merely sealed over.

One species of terrapin, namely *Clemmys leprosa* of Europe, is subject to a peculiar disease when living in foul waters, although perfectly healthy when frequenting clear streams; it is from this diseased condition that it derives its name of *leprosa*, or "leprous". When living in slimy pools an alga makes its way into the cracks and crevices in the horny plates of the shell, and thus penetrates into the underlying malpighian layer of the skin, or even into the bone itself, which becomes gangrenous in large patches, while the whole shell has a distinctly leprous appearance. The only other known instance of an alga flourishing in the superficial tissues of a vertebrate animal occurs in the sloths (*Bradypodidæ*) among mammals, where it grows in the grooves traversing the coarse hairs, to which it communicates a distinct greenish tinge, believed to aid in rendering the animal inconspicuous in its leafy haunts.

All vertebrates apparently change from time to time their epidermis and its appendages. In some cases, as in the human

species, the change is gradual and imperceptible. In other instances the shift is more marked, as in the changing of the hair in many mammals in spring and autumn, and the "moult" of birds. In certain reptiles—namely snakes and lizards—(as well as in amphibians) alone is the entire epidermis, inclusive even of that covering the cornea of the eye, sloughed at once, either, as in the case of snakes, entire, or in several pieces. In describing the change of skin in the common slow-worm, Dr. G. Leighton, in his "British Lizards" writes as follows:—

"The slough is exceedingly delicate and therefore torn with great ease, and can only be shed entire if the slow-worm is able to glide through soft material during the process of changing. Any sharp projecting point rubbing against the sides of the creature will inevitably tear the slough before it is completely removed. The process starts at the jaws, and the lizard gradually crawls out of the slough, leaving it turned inside-out as a rule, though the terminal portion of the tail-slough may slip off unreversed. After sloughing, the slow-worm, like other reptiles, is more lively and feeds readily. The length of time between successive sloughings varies. Sloughing always happens after the slow-worm comes out of its winter-quarters, and is generally repeated at intervals of six weeks or so during the months in the year when active life is in progress. The colouring of the reptile is more brilliant after sloughing than at other times. The slough is never eaten by lizards [and snakes], as is the habit of some amphibians."

The number of times in the year in which certain Indian snakes shed their skins while in captivity is recorded on p. 48; and in these it would seem that the change is less frequent than in the slow-worm. In tropical countries it is no uncommon thing to find the complete slough of a python or other large snake from 6 to 10 feet in length.

In terrapins, and probably in other chelonians as well, a more incomplete, although at the same time a well-marked, change of the superficial layer of the skin takes place. In the case of the freshwater painted terrapin (*Clemmys picta*), for example, a thin transparent layer, like a film of mica, peels off all the heavy plates of the shell in autumn or at midsummer, when the brilliant colours underlying the newly formed plates appear much more vivid than ordinary.

Although no reptiles live in organised communities after the fashion of hamsters among rodent mammals and bees and ants among insects, there are a few instances of certain species living in companionship with other animals. In North America, for example, rattle-snakes frequently take up their residence in the burrows of the "prairie-dogs," or prairie-marmots (*Cynomys*), which are often also tenanted by the curious little owls of the genus *Speotito*. It used to be supposed that these strangely associated animals constituted a veritable "happy family," but it is now ascertained that the snakes resort to the marmot-warrens for the sake of feeding on the young marmots. When there are no young ones, it would, however, seem that the snakes live in a state of harmony—or at all events of "armed neutrality"—with the marmots.

Another instance of a similar kind of association is afforded by the New Zealand tuatera (*Sphenodon*), whose burrows are sociably shared by petrels of various kinds. The petrel is stated to usually occupy the left, and the tuatera the right side of the inner chamber of the burrow, which, by the way, is invariably excavated by the reptile. The late Sir J. von Haast observes that while very tolerant of the bird and its young, the tuatera does not allow another reptile of its own kind to live in the same hole, which it is ready to defend by lying in such a manner that the head is placed where the passage widens out to form the chamber.

Another curious association between a bird and reptile occurs in Egypt. Herodotus tells the story that a bird he called *Trochilus* enters the open mouth of a basking crocodile to pick the fragments of food left between the teeth of the reptile. For a long time this story was rejected as a "traveller's tale," but modern observations appear to show that it is perfectly true. At one time the bird in question was supposed to be the black-backed courser (*Pluvialis aegyptiacus*), but it really appears to be the spur-winged lap-wing, or zicza (or *Hoplopterus armatus*). An observer writing in 1870 stated that he saw a bird which he believed to belong to the latter species deliberately enter the mouth of a basking crocodile two or three times; and that during one of these visits the reptile actually closed its mouth, opening it again after a time to let the bird out.

## CHAPTER V

### SEX AND REPRODUCTION

Some sexual features. Cries. Scent and scent-glands. Milky and other secretions. Significance of brilliant colouring. Habits in breeding season. Reproduction and care of eggs and young. Maternal instinct in pythons. Vipers swallowing young. Fertility of snakes. Incubation.

INFORMATION is still deficient with regard to the behaviour of the two sexes of reptiles during the breeding season, although a few observations have been recorded which show apparently that in the case of some species at any rate much excitement, frequently accompanied by pugnacity, is displayed at this period. A few kinds develop specially brilliant colours, or an intensification of the normal colouring; but since many reptiles, or, at all events, many snakes and lizards, are at all times more or less brilliantly coloured, and likewise show variations in the brightness of their hues according to whether they have recently changed their skins or not, it is difficult to decide to what extent any or all of the brilliant tints displayed by certain species during the breeding season are due to what is commonly called sexual selection.

In a large number of instances male and female reptiles are very similar to one another in general characters; but in other cases there are marked secondary sexual differences between the two sexes. For example, many male lizards are more brightly coloured than the females, and often show special patches of colour which are wanting in the latter. Again, in the family of the *Iguanidæ* there is often a greater development of the characteristic dorsal crests and gular pouches, or "dew-laps," in the males. For example, the male basilisk (*Basiliscus americanus*) alone possesses the tall sail-like crest running down the back and tail; and it is only the male of the horned iguana (*Metopoceros cornutus*) which carries the three horn-like scales on the forehead characteristic of the genus and species.

Similarly, a dewlap is developed only in the males of the chamæleon-iguana (*Anolis carolinensis*). Among geckos the males are generally larger and distinguished by the presence of femoral pores. Among crocodiles the males of the Indian gharial (*Garialis gangeticus*) are distinguished by the presence of a large swelling at the extremity of the snout, enclosing the nostrils. When the nostrils are closed, this swelling can be blown out like a football: probably connected with this organ, which is doubtless of a sexual nature, is the presence on the base of the hinder part of the skull of a pair of large bony capsules, of the size of a hen's egg, and connected with the respiratory passages.

Perhaps, however, the most remarkable secondary sexual difference in reptiles occurs among the Chelonia in the terrapins and land-tortoises. In all these the male, which is generally much the larger of the two, has the centre of the plastron, or lower shell, more or less deeply hollowed, whereas in the female it is flat or even slightly convex. The object of this hollowing of the plastron in the male is so obvious that it need not be particularised. Male tortoises have also longer tails than females.

Closely connected with the sexual function are the cries uttered by many reptiles, more especially in the breeding-season. In the common *Testudo græca*, for instance, the male, which then becomes unusually alert and active, makes a kind of piping noise when in pursuit of the female during the breeding season. Again, during the pairing-season the males of the giant land-tortoises of the Galpagos Islands utter a hoarse roar, or bellow, which can be heard at a distance of over a hundred yards. The female never uses her voice (even if she has one), and the male only at pairing-time; so that when the natives hear the sound, they know that the two are together.

Certain terrapins, such as the pond-tortoise of Europe and the species of the Asiatic genus *Nicoria*, can give vent to a kind of whistle. It is, however, a comparatively recent discovery that the males of most members of the American family of terrapins typified by the so-called "stinkpot" (*Cinosternum odoratum*) are in the habit of producing musical notes after a fashion very similar to that obtaining among grasshoppers and crickets. These terrapins are furnished with two patches of

horny tubercles on the hind legs, which afford good specific characters. As in crickets, there is an active and a passive set of these tubercles, the lower patch being rubbed against the upper one, and thereby producing a musical note, as does the bow of a violin. The note is clear and distinct, audible at a considerable distance. As the tubercles are developed only in the males, they are probably used to produce musical notes solely during the breeding season, thereby informing the females of the proximity of members of the opposite sex. These musical instruments of the *Cinosternidæ* are almost unique among vertebrates; the only other instances of the development of a somewhat analogous apparatus in that group occurring among the geckos of the genera *Teratoscincus* and *Ptenopus*, which are enabled to produce musical notes by means of friction between the horny rings of their tails. This sound, which is like the chirping of grasshoppers, is, however, emitted by both sexes, and may be for the purpose of attracting those insects within reach. Very probably, the clicking cry of other geckos is, at least in part, of a sexual nature, and likewise the chirp of lizards. Chamæleons both hiss faintly and grunt; but these sounds are probably uttered for the purpose of frightening enemies, as is certainly the case with the hissing of serpents and monitors.

It is by no means easy, as in the case of cries, to determine in all instances whether scents (or their opposite) are for the purpose of attracting the individuals of a species or for repelling enemies. If, however, the sense of smell in reptiles is akin to that in ourselves, it may be presumed that agreeable scents are connected with the sexual function, while disagreeable ones are for the purpose of repelling enemies. Under the former category probably comes the musky odour exhaled by crocodiles from two pairs of glands, one of which is situated on the throat and the other near the vent. The scent, it has been suggested, leaves a musky aroma along the line of water traversed by the animal, by means of which another individual is enabled to ascertain its whereabouts.

On the other hand, the exceeding ill-smelling odour exhaled by *Clemmys leprosa* and certain other terrapins and tortoises can scarcely be regarded in any other light than as a defence against enemies. In this instance the secretion, which is de-

scribed as something like concentrated essence of fish, is the product of a pair of glands situated beneath the skin near the inguinal region, and opening on each side behind the bridge connecting the upper with the lower shell. Freshly caught specimens of this species, according to Dr. H. Gadow, stink horribly when handled; but after they have been kept in confinement for some time, they lose the habit of voiding the contents of the glands every time they are taken up, and thus become less objectionable pets.

The North American "stinkpot-terrapin" (*Cinosternum odoratum*) owes its ill-favoured name to the fetid secretion exuded by the inguinal glands, which can scarcely be regarded as intended otherwise than as a means of defence.

Under the same category must doubtless come the habit displayed by certain lizards (such as the scheltopusik) and snakes (among them the common ring-snake) of ejecting when handled the ill-smelling contents of the cloaca.

The milky fluid exuded by the American milk-snake and the blood squirted from the eyes of the so-called horned toad, to which fuller reference is made in the concluding chapter of this section of the present work, likewise come under the category of fluids discharged for defensive purposes, whether used in combat with rival males for the possession of some coveted female, or to repel the attacks of enemies of another kind.

Many lizards inflate the body, the region of the mouth, or special laryngeal sacs, for the apparent purpose either of frightening enemies or as a means of sexual attraction, or perhaps for both together. Examples of this are displayed by the inflation of the body in *Lacerta* and *Phrynosoma*, in the expansion of the frills of *Chlamydosaurus*, and the dilatation of the gular sacs of *Metopoceros* and other iguanas. Such effects might be enhanced, it is reasonable to suppose, by a swelling-out of the head and protrusion of the eyes. Such a function, according to Dr. H. L. Bruner in the *American Journal of Anatomy*, vol. vii., pp. 1-117, is, however, insufficient to explain the existence in the heads of both sexes of many lizards and snakes of an apparatus of muscles and vascular sinuses for producing excessive blood-pressure, and consequent swelling in this region. In lizards, at any rate, this mechanism

is developed for the purpose of aiding in the shedding of the scales, and acts physiologically by accelerating lymph-movements, and thus promoting metabolism, and mechanically by stretching the skin over the soft parts. This being so, the probability is that the same factor holds good in the case of snakes and tortoises ; but in some instances the function may be modified for terrifying or sexual purposes, and it is probable that the ejection of blood from the eyes of the "horned toads" (*Phrynosoma*) is a development of the same mechanism.

From the foregoing it is clear that it is necessary to be guarded in framing any hypothesis as to the precise significance of brilliant coloration among reptiles. Though commonly associated with sexual display, it does not seem always to be used as an accessory in this respect.

A case in point is furnished by the painted terrapin (*Chrysemys picta*). In the breeding season the male has been seen dodging the female, and making efforts to oppose her path. This end accomplished, the male closed up and immediately commenced to beat a lively tattoo with his long finger-nails upon her head and eyes, the movements being so rapid that nothing more than a blurred image was possible. So soon as possible, the female escaped these attentions, when the male set about repeating the performances, which were witnessed not once but many times before the pair were disturbed and made off. Here no use seems to have been made of the bright coloration but only one phase of the "display" may have been observed.

Crocodiles find a sombre livery useful, since it affords concealment. Consequently the males present, except in the case of the gharial, no ornamental colours, nor any other marked secondary sexual character. Nevertheless, alligators, when endeavouring to attract the females, splash, roar, and twist themselves around on the water, with the head and tail raised, and the body inflated to its utmost extent, the effect of this being increased by the emission of a strong odour of musk from glands in the lower jaw.

In many lizards the males display great pugnacity during the breeding season, and rivals never meet without a conflict. In *Anolis carolinensis*, for example, when two males meet they face one another, bob the head up and down two or three times

expand a great throat-pouch they possess, lash their tails from side to side, and then, worked up to the requisite pitch of fury, rush at one another, rolling over and over, and holding firmly with the teeth. The conflict generally ends by one of the combatants losing his tail, which is eaten by the victor.

Dr. Gadow states that in the breeding season the males of a Malay lizard (*Calotes emma*) "are very pugnacious and change colour as they fight. At the time of courtship a curious performance is gone through by the male, the females remaining concealed in the foliage hard by. He chooses some convenient station such as a banana leaf, or the top of a fence, and advances slowly towards the female. His colour is then pale yellowish flesh-colour, with a conspicuous dark spot on each of the gular pouches, which are extended to their utmost. He stands upright, raising the fore part of the body as high as possible, and nodding his head up and down. As he does so, the mouth is rapidly opened and shut but no sound is emitted. When he is driven away, caught or killed the dark spot disappears entirely from the neck."

That instances of this kind are by no means rare there can be no doubt, but records of actual observation are few. Those cited show the nature of the evidence so far collected, but on the whole there is less activity and intensity of feeling displayed by reptiles in their choice of mates than is the case with birds.

Similarly, in the care displayed for their offspring reptiles are far behind birds. As already mentioned, reptiles are properly oviparous, laying eggs from which the young are usually hatched by the heat of the sun or by that engendered by decaying vegetable matter, without any aid from either parent. In many species, however, such as the common viviparous lizard (*Lacerta vivipara*) the young burst the shells of the eggs immediately after they are laid, or in some cases even before they are laid. Although in the latter instance the species may be said to be viviparous, the term ovo-viviparous is properly applicable to this mode of reproduction. At least one reptile, namely the Australian stump-tailed lizard (*Trachysaurus rugosus*) is, however, really entitled to be called viviparous, for not only are the young born free, but the hard calcareous shell characteristic of the eggs of reptiles in general is never developed. These differences in the mode of reproduction are probably in all cases

correlated with some special feature in the life-history of the species in which they occur, and are therefore mainly, if not entirely, adaptive, although in most instances the reason for such adaptation is not apparent. In the case of the sea-snakes (*Hydrophiinae*), however, which are viviparous, the reason for the departure from the normal oviparous mode of reproduction is plain, as these reptiles, unlike turtles, never voluntarily come to land. The burrowing snakes of the families *Illysiidae* and *Uropeltidae*, and possibly also the *Typhlopidae*, are likewise viviparous; and here again the reason for the specialisation is not very difficult to discover. On the other hand, it is not easy to see why the viper (like most of its tribe) should be viviparous, while the ring-snake is oviparous.

Till a few years ago most of the viper tribe were believed to produce their young alive; that is to say, the eggs are hatched within the body of the female parent, so that, strictly speaking, these reptiles should be described as ovo-viviparous rather than viviparous. In the *Field* of January 1, 1910, there appeared, however, a letter from Mr. C. Leigh in which it is stated that the Himalayan pit-viper (*Lachesis monticola*) is oviparous. This viper, which ranges from the Eastern Himalaya to the Malay countries, is remarkable for the great thickness of its body as compared with the length; for while it usually attains a length of about  $2\frac{1}{2}$  feet, its girth is sufficient for that of an average 5-foot snake. The ground-colour of the back is ashy-grey, upon which is a series of more or less regular dark blotches, with a sprinkling of black and traces of yellow. On the under-parts the general colour is likewise ashy, but with dark red mottlings. In some examples the dark markings on the upper surface are so pronounced that the reptile is scarcely distinguishable from the freshly-turned black soil of the tea-gardens, in which it is frequently found. It was while working in a garden at Kurseong, during the summer of 1909, that a coolie came across a cluster of snake's eggs. On reaching out his hoe to investigate and pushing the grass aside, he discovered a viper of this species which made a snap at him, but was eventually secured. The tropical American bushmaster (*Lachesis muta*), and all the members of the African genus *Atractaspis* are also oviparous.

An analogous instance is offered by the family *Boidae*, in

which most of the boas produce living young, while pythons lay eggs. A still greater difficulty arises (as in the case of *Lachesis* and *Lacerta*) when we find the two modes of reproduction occurring respectively in different species of the same genus. The North American banded water-snake (*Tropidonotus fasciatus*) belongs, for example, to the same genus as the egg-laying ring-snake, and yet produces living offspring.

In some instances among lizards all or most of the members of a family may be oviparous or viviparous as the case may be; but in other instances there is a strange mingling of the two types of reproduction. The iguanas, for example, appear to be, at least for the most part, oviparous, while the skinks are as markedly viviparous. On the other hand, the above-mentioned viviparous lizard stands out as a marked exception among an oviparous group; while in the family *Anguidæ* we find that whereas the continental glass-snake, or scheltopusik (*Ophisaurus*) lays eggs, the British slow-worm (*Anguis*) gives birth to living offspring.

All crocodiles, together with chelonians and the tuatera, are oviparous.

Of the modes of reproduction of fossil reptiles we are, from the nature of the case, in most instances ignorant. By what may be regarded as a fortunate accident, we know, however, that the ichthyosaurs produced their young alive, after the manner of sea-snakes. The evidence for this is afforded by certain skeletons (of females) from the German Lias, within the ribs of which are enclosed the remains of foetuses. This departure from the normal type of (oviparous) reproduction is evidently correlated, as in sea-snakes, with more or less completely pelagic habits; and thus indicates, as might have been expected from the structure of their paddles, that the typical ichthyosaurs never came ashore, but led lives similar to those of whales; the pelagic habit being most developed in the specialised *Ophthalmosaurus* of the Oxford Clay.

Whether plesiosaurs, pelagic crocodiles, and sea-serpents (mosasaurs) were likewise viviparous, or whether, like turtles, they came ashore to lay their eggs, cannot be positively stated. On the one hand, the less specialised type of paddle (as compared with the ichthyosaurs) might lead to the inference that these reptiles occasionally came to land. On the other hand,

the snake-like form of the body in the mosasaurs, coupled with the weakness of the pelvis, and the extreme length of the neck in the plesiosaurs (which would appear to be exceedingly inconvenient to an animal on land), suggest a completely aquatic life for the members of those two groups. If this be a true inference, there can be little doubt that they were viviparous.

One other adaptive modification in the ichthyosaurs may be mentioned. From their "coprolites" it is known that they were furnished with a spiral valve to the intestine; a feature paralleled by sharks, rays, and chimaeras among fishes. Ichthyosaurs also resembled sharks and many dolphins in possessing a dorsal and a caudal fin; the latter being, like that of sharks (and unlike that of dolphins), vertical.

There are remarkable differences in the shape of the eggs of reptiles, some being spherical, while others are elliptical, with the two ends symmetrical; in no case, however, do we find the typical "egg-shape," that is to say, one end rounded, and the other more or less pointed. Crocodiles and gharials lay elliptical eggs about the size of those of a goose; but the tuatera's eggs are spherical. Pythons' eggs are also spherical, while those of many other snakes are elliptical, and fastened together in bunches or strings. Many land-tortoises, again, lay spherical eggs, which in the case of the giant species are about the size of lawn-tennis balls; and the eggs of the marine turtles are similarly shaped. On the other hand, the fresh-water terrapins and batagurs lay elliptical eggs. The season for this diversity in shape is difficult to discover, seeing that it has no correlation with terrestrial or aquatic habits.

As already mentioned, most reptiles leave their eggs to take care of themselves after they are laid. The sand-lizard (*Lacerta agilis*), for example, deposits its eggs, which usually range from five to eight in number, during July in a depression in sandy soil, where they are left to hatch by the aid of moisture and the sun's heat. In cases, however, where sand is not to be found the eggs are deposited in leaves, vegetable mould, or rubbish. In the case of the green lizard (*L. viridis*) the eggs, generally eight to ten in number, are developed for five weeks within the maternal oviducts, and are then laid in suitable situations, where they remain four weeks more before they hatch. The ring-snake usually selects decaying vegetable

matter, or, in gardens, manure-heaps, in which to deposit its clusters of eggs.

Turtles lay their eggs in holes scraped out in the sand of tropical coasts well above high-water mark to the number of a hundred or more; the holes being carefully filled up with sand and the surface smoothed down. The period of incubation, by the aid of the sun's heat, is believed to be at least seven weeks. Turtles' eggs have a parchment-like covering, unlike the hard calcareous shell of those of the giant land-tortoises.

Crocodiles likewise generally lay their eggs in sand, and leave them to be hatched by the sun's heat, although, in some cases at any rate, they are visited from time to time by the female parent, who assists the young ones in escaping from their prisons. In the case of the Nile crocodile (*Crocodilus niloticus*) in Madagascar, the eggs are laid in a pit in the sand from one and a half to two feet in depth; the centre of the pit being rather higher than the margin, which is undermined, so that the eggs naturally roll into the shelter thus formed. The eggs are laid somewhat before daybreak; and after half the batch has been deposited, a layer of sand is spread for the reception of the moiety. When the laying is completed the pit is filled up with sand and the surface smoothed down. The position of the nest is, however, frequently betrayed by the mother taking up her position upon it at night. When the young are hatched (which occurs in about twelve weeks after the laying of the eggs), the nest is generally pulled to pieces, and the empty egg-shells left lying scattered about. This digging out of the nest is believed to be accomplished by the mother, who appears to be warned when the eggs are ready to be hatched by the piping cries uttered by the young crocodiles while still in the shell. Apparently the eggs are dug out by the parent several days before they actually hatch. The process of breaking the shell is accomplished by the young crocodile with the aid of the "egg-tooth"; a two-cusped excrescence on the summit of the upper jaw at the extremity of the muzzle; this acts in drill-fashion, and does not disappear till some weeks after birth. Many other reptiles have a somewhat similar weapon.

In tropical America the female of the black caiman (*Caiman niger*) covers up her eggs with a mass of bushes, and

keeps guard close by till they are ready for hatching, when she probably assists the young ones to escape.

In pythons the maternal instincts are still more developed, and the female incubates, or rather coils herself round (for no augmentation of temperature occurs), her pile of eggs until they hatch. The object of this action is probably in the main, if not entirely, to protect the eggs. A female python in the London Zoological Gardens brooded her eggs for some weeks in this manner in the summer of 1881.

Unfortunately, the observations made in the foregoing instance were imperfect, practically the whole information obtained being that the snake coils herself round the mass of eggs to protect them and that no appreciable amount of extra warmth is developed during incubation. A second instance of a python laying and brooding eggs in captivity has been more recently recorded in Ceylon. In the autumn of 1904 a python (probably *Python molurus*) was received at Colombo from the Malay Archipelago. Although the measurements and weight could not be ascertained, it is estimated that the snake was about 28 ft. in length and weighed 250 lb. Soon after its arrival from Singapore—that is to say, on 28th October—the snake laid about 100 eggs, which almost filled the box in which it was kept. On the following morning, by skilfully coiling her body around them, she had collected the mass of soft-shelled eggs into a heap in such a manner that they were almost completely covered without being pressed by the weight of her body. In order apparently to maintain a constant temperature the python from time to time partially uncoiled herself, so that the heap of eggs became visible. From 28th October, 1904, till 14th January, 1905, she refused all nourishment, although tempting dainties were offered. On the latter date the python left the mass of eggs exposed, and it was feared that incubation had been unsuccessful. Closer inspection revealed, however, a young python half emerged from one of the eggs, into which it retired at evening. On the next day, 15th January, six young pythons were hatched, some of which died in a few hours, while the others soon became active, making darts at a cloth held near them. Eventually forty-five young snakes were counted, of which thirty-six were alive on 20th January. When first hatched the young measured 2 ft. to  $2\frac{1}{2}$  ft. in length. The period

of incubation of the Malay python is thus two and a half months.

Another instance of a python (this time an African species) incubating in captivity occurred in the Jardin des Plantes, Paris, in the year 1841. A fourth case took place in the menagerie at the Tower of London in the year 1828. In this instance the snake had been more than two years in the collection when she produced fourteen or fifteen eggs, none of which, however, were hatched, although the mother evinced great anxiety for their preservation, coiling herself round them in the form of a cone, of which her head formed the summit, and guarding them from injury with solicitude. The eggs appear to have been shown to visitors by the keeper, for it is stated that they were only visible when she was occasionally roused, and raised her head, which formed the cover of the pile. Every time, however, she resumed her normal position as quickly as possible, allowing the spectator only a momentary glance at her treasures.

If there be any truth in the story of its swallowing its young, the most remarkable instance of maternal care among reptiles occurs in the viper. On the face of it, this occurrence seems sufficiently improbable, and its possibility has been denied. Nevertheless, popular beliefs are often founded on fact. The question has been considered by Dr. G. Leighton; and although he has been unable to cite any definite instance of the occurrence of the phenomenon, he shows that some of the objections which have been urged against it are based on a misinterpretation of anatomical facts, and demonstrates that there is nothing impossible in its taking place. As the gullet of an adder is perfectly capable of containing the body of a field-mouse, and as frogs are known to live for a considerable time after being swallowed by snakes, there is no reason why young adders should not be swallowed by their parent without being killed. The question remains, however, to be proved by positive evidence. "Of the possibility of the phenomenon," writes the author, "we have not the slightest doubt, of the probability of it we have considerable doubt".

In the case of the python at Colombo about one hundred eggs were laid. In this great fertility pythons apparently are ahead of viviparous snakes, although exact information regarding the

maximum number produced by different species of the latter is still required. In 1906 I received the skin of a female of the beautifully-coloured Gabun viper, or puff-adder (*Bitis gabonica*), together with several young ones taken from the body when the reptile was killed. These young ones measured about twelve inches in length, and the total number was said to be thirty. Thirty feet of young snakes is certainly a goodly family, and confirms current statements as to the abundance of these deadly reptiles in the forests of equatorial Africa. The number of young produced at a birth by adult females of the European viper is stated to be generally from twelve to fourteen although, occasionally reaching sixteen. Younger females, however, produce only five or six at a time.

The North American banded water-snake (*Tropidonotus fasciatus*) seems to be an unusually prolific species, a female in the New York Zoological Gardens having on one occasion given birth to sixty-two young—a family so numerous that if literally overran the cage in a mass of writhing brilliantly coloured bodies.

Usually, it seems, the eggs of reptiles are hatched within comparatively few weeks of being laid. A remarkable exception is, however, afforded in the case of the New Zealand tuatera, which is in so many ways strange and aberrant. Although the eggs are laid during the summer (of the southern hemisphere), that is to say, from November till January or February, and contain fully developed embryos by the following August, they are not hatched till about thirteen months after being laid, thus coming into the world in summer. During the period of delayed development the embryos appear to undergo a kind of hibernation; the cavity of the nose becoming blocked by a growth of tissue which is absorbed as the time of hatching approaches. The eggs are not laid in the tuatera's burrow but in a warm sandy spot, where they may receive the full advantage of the sun's rays.

## CHAPTER VI

### COLORATION AND ITS INTERPRETATION

Colour in relation to environment. Stripes and spots in lizards. Colour-changes in relation to sex and age. Colours of young pit-vipers. Voluntary colour-changes. Green arboreal snakes. Desert-snakes. Sea-snakes. Bark-geckos. Lizards. Warning and protective colours.

UNLIKE the majority of mammals inhabiting the temperate and sub-arctic zones, reptiles do not exhibit a seasonal change of colour; and for the reason that they do not inhabit the sub-arctic regions, and that those of the colder parts of the temperate regions hibernate. It is noticeable, however, that the young of some reptiles are more brilliantly coloured than the adults, while snakes display much more vivid hues immediately after changing their skins than at other times. Probably the colours of the great majority of reptiles are protective, that is to say, they harmonise more or less completely with their environment, and thus render the creatures inconspicuous. For instance, foliage-haunting reptiles such as chamæleons and tree-snakes are coloured green; while the majority of reptiles inhabiting open ground are either mud-coloured or sand-coloured, as, for instance, crocodiles, stellion lizards, skinks, and desert-snakes. The brilliant coloration of many of the pythons, such as the Malay *Python reticulatus*, appears highly conspicuous in specimens in a museum, but it is probable that among the splashes of sunlight and shade of their native forest's these bright-hued reptiles are inconspicuous, the tessellated pattern of the colour breaking up the hard outlines of the body. Again, as is shown later, sea-snakes display adaptive colouring in a marked degree. Before considering in detail these adaptations in general colouring, reference may be made to observations with regard to the occurrence of stripes and spots in certain lizards.

Many lizards, especially some of the skinks, display a longi-

tudinally striped type of coloration. Such stripes occur in the European wall-lizard (*Lacerta muralis*); but they are by no means constant, and it appears that in certain cases a different colour-pattern may be assumed, according to age, and perhaps locality. Moreover, when such changes of pattern take place, they appear to do so in a definite order, which is generally as follows. First of all there are longitudinal stripes; next these stripes break up into spots, which may again coalesce into cross-bars; while, as a final change, all markings may disappear, and leave the skin uniformly brown or sandy. Certain individuals of this species undergo all these changes of colour and pattern as they pass from youth to old age; while others stop short at the second or even the first stage, and a few skip the first or second stage and begin life in the third or fourth. As a rule, these changes are most pronounced in the males; the females commencing the change at a later period of life than their partners, when they may either undergo the whole transformation or only pass through some of the stages. In all cases these changes of pattern and colour commence near the tail and advance forwards in a kind of wave-like manner, so that the shoulders of an individual of the species may be in one of the intermediate stages while the tail has attained the permanent sandy condition.

Very similar changes also take place in certain tropical American lizards of the genera *Cnemidophorus* and *Ameiva*, belonging to the family *Teiidae*, which is related to the iguanas. In these lizards a pattern of longitudinal white stripes not infrequently breaks up into spots; this dissolution commencing at the tail, and gradually advancing towards the head. On the other hand, pale spots may by confluence produce longitudinal light stripes. Another mode by which such stripes are produced is the concentration of dark pigment along the borders of a pre-existing dark band, accompanied by the growth of new colourless tissue in the middle of such band; thus giving rise to one white stripe flanked by a pair of dark ones. A modification of this process occurs in the case of the white dorsal streak met with in some lizards, which as it broadens tends to develop dark pigment along the middle line, and thus eventually becomes split into a pair of white stripes divided by a single dark one. Confluence of pale spots in a

transverse direction, accompanied by the deposition of dark pigment along the forming borders, leads to a pattern of transverse bars, corresponding to the third stage in the colour-evolution of the wall-lizard; while by the disappearance of both spots and bars the final uniform coloration is reached.

In these American lizards, as in the wall-lizard, there appears to be no doubt that the longitudinally striped condition was the original one; the spotted type being a secondary condition, from which have been evolved the cross-barred and finally the uniformly coloured stage. And as these changes are more or less paralleled both among birds and mammals, it may be definitely accepted that stripes and spots are more ancient than a uniform colour.

As regards the reason for these changes, it has been observed that if we start with the original and typical form, marked with six strongly pronounced white stripes, it will be found that in individuals frequenting sandy districts dotted with sparse tufts of grass there is a tendency to an increase in the number of stripes, of which there may be from eight to eleven. On the other hand, in neighbouring spots, where the vegetation is more abundant, the number of stripes is usually from seven to nine, and these show a tendency to break up into spots on the hind part of the back. As we pass into open tropical forest with much undergrowth the lateral stripes fade, while the others dissolve into spots which have a tendency to disappear on the loins in old individuals. Again, in races inhabiting open table-land with scattered spiny shrubs and hedges, the young form with six light stripes and pale spots on the dark bands tends to pass into a cross-barred type. Finally, in similar localities to the last, but with more mixed vegetation, all the lines become broken up into spots, in addition to those which existed in the intermediate dark intervals.

These changes appear to be correlated with the varying distribution of light in the different stations these lizards respectively frequent. If this be so, the colour-changes are protective in their nature; and it has been urged as a reason for the frequent elimination of the original white striping that the effect of such an arrangement is constantly interfered with by the movements of the animal. Further, it has been pointed out that it is far more natural for the lights and shadows to fall

transversely, rather than longitudinally, on a cylindrical body. As to the question why any of these lizards retain their longitudinal striping, seeing that it is the natural course of evolution that they should be lost, it has been suggested this may be due to the circumstance that small-bodied reptiles living among sparse tufts of grass have their colour-pattern less interfered with than is the case with their larger relatives, or even that the incidence of sunlight enhances the effect of their linear marking. It appears indeed that these lizards cannot retain their stripes unless they live in situations where such a type of coloration tends to render them in harmony with their surroundings; any more than they keep their pale spots amid desert surroundings. For it is a well-ascertained fact that when spots occur in desert-dwelling animals they are dark on a light ground, as is exemplified among reptiles by some of the sand-skinks (*Chalcides*) and among mammals by leopards and servals; while among forest-dwellers light spots on a dark ground are the fashion, as in the fallow-deer and the Indian spotted deer.

It may be taken, then, as probable that most of the uniformly coloured or dark-spotted reptiles inhabiting desert districts, where their coloration is eminently protective, are derived from white-striped or white-spotted ancestors dwelling in situations where vegetation was more or less abundant. And if this be true, it follows that chamaeleons and tree-snakes which have acquired a green livery to harmonise with the surrounding foliage have in all probability been evolved from striped or spotted ancestors by an analogous modification. Be this as it may, such green coloration in arboreal reptiles is evidently a specialised protective adaptation, as is likewise the colour-charge of chamaeleons and certain lizards.

Exemplifying somewhat more fully the variations in colour and pattern which occur in many reptiles, it may be shown to what extent these are connected with sex and age in species other than those already mentioned.

As an example of sexual colour-difference may be cited the terrestrial iguanas of the genus *Sceloporus*. In most of the numerous representatives of the group the males are larger and more brilliantly coloured than the females, from which they are further distinguished by the presence of bright blue blotches

on the under-parts. These blue blotches, and the brighter tints generally, being placed on the under surface of the body are more or less completely hidden when the reptiles are crouching on the ground, and only become visible when the head and body are elevated under the influence of excitement. At such times the blue or purple on the throat of the males is conspicuous, although that on the flanks is less noticeable. This type of colouring is therefore evidently a secondary sexual character. Generally the upper parts are some shade of brown, and adapted for protective resemblance when the lizards are crouching. Here it may be noticed that the bright blue spots on the flanks of the European eyed lizard (*Lacerta ocellata*) have the same situation as the lateral blue blotches of the males of *Sceloporus*; and if, as is probable, they are brighter in males than in females, they may be regarded as sexual colour-features. From their position, it may be inferred indeed that these blue blotches have little to do with concealment although, as already mentioned, the "vermiculated" black and yellow colour-pattern of the back of these lizards is protective. Still, as stated below, the whole colouring may at a short distance blend into an inconspicuous blur.

The American blue-tailed skink (*Eumeces quinquelineatus*) offers an example of pattern and colour-change dependent upon sex and age. In the young the tail is bright blue and the body blackish with five yellow stripes. As this lizard matures the tail fades to sombre grey, the body changes from black to brown, the stripes (in the males at any rate) entirely disappear, and the head, in the same sex, assumes a bright red hue. Formerly the adult was regarded as a distinct species.

Again, in the aforesaid terrestrial iguana, *Sceloporus zosteromus*, the adults show a broad dark lateral band running backwards from in front of the fore-limb along the flank, while in the young the large patch in front of the fore-leg is frequently disconnected from the lateral band. In *S. biseriatus* the throat, the middle of the under surface, and the lower side of the thigh in old males are often black, while in younger individuals they are greyish or bluish. In the case of one species of horned toad (*Phrynosoma coronatum*) all the markings are much more distinct in the young than in the adult; the small spots on the raised portion of the scales of the head in the young gradually

increasing in size until the whole crown becomes dark brown or blackish, crossed by irregular yellow lines marking the hind borders of the scales. In the allied *P. platyrhinus* the markings on the hind part of the back are apt to become obsolete in the adult. Another type of variation has been recorded in the Mexican poisonous lizard (*Heloderma suspectum*), in which the dark rings on the tail and limbs of the young break up into irregular spots in the adult. The lizards of the genus *Gerrhonotus* exhibit in a marked degree the more brilliant colouring of the young, and also show in that condition a distinct pattern of alternate light and dark bars which tends to fade out as maturity is attained. The age and sexual differences in colour and pattern in the genera *Ameiva* and *Cnemidophorus* have been already noted.

Perhaps, however, the most remarkable colour-change of this type occurs in an African snake known as *Grayia ornata*. In the young of the phase described as *Grayia ornata furcata* the body is black with broad whitish or greyish transverse bars, which split on each side so as to form a series of reversed Ys; each Y being slightly speckled with black about the middle line. With advancing age the black ground changes to grey or brown; whereas the Ys show more and more black until they have only white margins, and even these eventually disappear. Consequently, the fully adult snake has black markings on a grey ground, in place of the light markings on a black ground characteristic of the young; in other words, the colour-pattern of the adult is precisely the reverse of that of the young.

In regard to colour-variation in British lizards the following observations have been published by Dr. G. R. Leighton in his *Life-History of British Lizards*.

"Very young specimens of *Lacerta vivipara*, the common lizard, are nearly black, while the adults are brown and spotted; the under-parts red or orange in the males with black spots, while in the females these portions are yellowish. The young of the sand-lizard, *L. agilis*, are greyish-brown with spots, whitish underneath; the adult male is typically green on the sides, the female more brown. In *L. viridis*, the green lizard, the yellow lateral stripes which are found in the young persist in some of the old females."

The same writer refers to the much brighter colouring of young vipers, as compared with very old specimens. A much more marked change in colour occurs, however, in the Malay snake known as Wagler's viper (*Lachesis wagleri*), which in the young state is generally green while in the adult it tends to blackish. The protective nature of this colouring, at least in the young condition, is referred to in the sequel. This viper also exhibits great variation in colour apparently independent of either age or sex. Neither does it seem that these variations are altogether local, seeing that both the first and the third of the under-mentioned colour-types occur in Borneo, while the first and fifth are recorded from Celebes. These variations, according to the British Museum *Catalogue of Snakes*, are as follows:—

“A. Green above, with white cross-lines edged behind with blue or purple, or with two dorsal series of small spots or cross-bars of the same colour; a white line on each side of the head, passing through the eye, edged below with blue or purple; belly white or pale green, with or without black edges to the ventrals; end of tail usually red or reddish brown.

“B. Green above, with small black spots or cross-bands; a black streak on each side of the head, passing through the eye; yellow beneath, with or without black edges to the ventrals, with a series of small black spots on each side; end of tail red.

“C. Yellowish green above, the scales edged with dark bottle-green; dark cross-bands of the latter colour; some specimens dark bottle-green above, with scattered yellowish green dots; ventrals yellow, edged with dark green, with a series of round green spots on each side, or dark green with yellow spots; end of tail dark green or blackish.

“D. Green above, with the scales black-edged, with bright yellow black-edged cross-bands, or black with yellow cross-bands; head black, spotted with yellow; belly bright yellow or yellow and green; ventrals black-edged; end of tail black.

“E. Green above, with large brick-red, black-edged spots; white beneath, with black spots and marblings powdered with brick-red; end of tail red.”

Such differences, whether they be individual, or characteristic of local races, demonstrate how easily new specific types can be evolved from existing forms.

In the New York Zoological Park some remarkable colour-

changes due to age have been observed in pit-vipers. These snakes are born with the tip of the tail, for the length of about an inch, of a brilliant sulphur-yellow. When food is introduced into the cage these young vipers communicate a writhing, twisting motion to their tails, causing the latter to resemble small worms, or maggots. Possibly nature has provided them with this dash of brilliant colour to attract small birds, lizards, or frogs within reach, as they lie coiled and difficult to discern from the surrounding vegetation. This feature has been observed in the copperhead snake (*Ancistron contortrix*), the water-moccasin (*A. piscivorus*), and the fer-de-lance (*Lachesis lanceolata*). After the first year, the yellow of the tail becomes very indistinct, and during the second year it disappears altogether.

With some of the pit-vipers, the colours of the young are very brilliant, although they exhibit much the same pattern as the adult. Young moccasins show brilliant shades of red and yellow at birth. The adults display a dull pattern of varying shades of sombre olive; while old specimens exhibit no pattern at all, the body being dull green.

Quite different from the pit-vipers are the young of some of the colubrine snakes. The young of the black snake (*Bascanium constrictor*) are pale grey, with blotches of brown or red along the back, and resemble the milk-snake (*Ophibolus doliatius triangulus*). During their second year they become darker, and the pattern appears diffused. The third year shows hardly a trace of the spots as the black of the adult appears, although the sides indicate the marking of the young.

The chicken-snake (*Coluber quadrivittatus*) is remarkable, as are most species of *Coluber*, in showing when young an entirely different pattern from the adult, both forms being strongly coloured. At the time of hatching the young chicken-snake is greyish, decorated with a regular series of oblong blackish saddles. As the reptile approaches maturity, the body-colours change to yellow, a dark stripe appears on each side of the saddle-like markings, and another on the side of the body. These stripes become very distinct before the saddles begin to fade. The latter change takes place usually during the third or fourth year, the mature form being uniform yellow or brown, traversed by four longitudinal stripes.

Apparently no reptiles assume a special coloration in the breeding-season comparable to the "nuptial pluīnage" of many cock birds, or to the brilliant tints of the male crested newt at the season in question.

The fact that chamæleons, which are for the most part uniformly coloured, have the power of changing the hue of their skins according to the nature of their environment has long been familiar, but it is less well-known that certain lizards are endowed with the same faculty. The colour-change in chamæleons is due to the presence of pigment-bodies deep down in the skin, which can be kept in that situation, or can be brought near to the surface at the will of the reptile. When the pigment is deep-seated, the skin appears dirty white or yellowish; when, on the other hand, it is allowed to come near the surface, the colour becomes dark or even blackish; while in the intermediate condition a greenish hue results from the diffusion of the dark colour through the outer layers of the yellowish skin, and by the iridescent character of certain elements in the latter.

The colour of the common chamæleon is practically indescribable, so great and so frequent are its liabilities to change, although there is great individual variation in regard to the frequency, duration, and extent of the changes. The normal coloration may be described as greyish green, with a number of darker specks and two series of pale brown patches on the sides of body, and a single patch near the ear. At night the prevalent hue is creamy yellow, with irregular blotches of yellow. Under the influence of excitement, as when in the act of striking a fly, the normal diurnal tints are intensified, the pale brown patches deepening to a full maroon, while the green is dotted with spots of golden yellow. Passion seems to cause these golden spots to turn blackish green. Very noteworthy, as showing the economy with which natural phenomena are conducted, is the fact that in many instances it is only the exposed side of the body that turns green when the animal is moving or sitting among foliage in daylight; the concealed side being yellowish white. Direct sunlight leads to a general darkening of the colours; and it is remarkable that in some instances the normal green hue, with or without the dark blotches, is retained during the night.

As chamæleons form a subordinal group (the Rhiptoglossa)

of the Squamata, it is evident that their adaptive green and changeable livery has been acquired independently of that of the chamæleon-iguanas (*Anolis*), which belong to the family *Iguanidae*. In the case of the Florida chamæleon-iguana (*Anolis carolinensis*) the extreme ranges of variation in colour extend from dark brown to pea-green; the former hue (in captive specimens at any rate) being assumed in daylight and the latter at night. The brown condition is induced by the migration of pigment-granules from the centres to the terminal branches and processes of the "melanophores"; the green state, which is one of rest, being the result of the withdrawal of the granules to the centres of the larger bodies. In three fundamental points this colour-change differs from that of the chamæleons; differences which are only natural to expect in phenomena of totally independent origin. When a brown anolis is placed in the dark, it invariably turns green in about five-and-twenty minutes, and when a green one is exposed to the light, it nearly always changes to brown in the short period of about four minutes. Marked differences in the length of time occupied in these changes have been recorded; and the change from brown to green is often slower at the commencement of an experiment than after it has been continued for some time. This leads to the conclusion that the period of colour-change is shortened by exercise, or practice; and it has been inferred that a low temperature induces a migration of the pigment-bodies towards the surface of the skin, while a high one is conducive towards their withdrawal. This rule appears to be constant for all reptiles subject to a colour-change. On the other hand, light sometimes follows this rule, and sometimes acts in the opposite manner.

For example, in certain monitors a strong light acts like a high temperature in causing a withdrawal of the pigment-bodies, while a dim light, or darkness, acts in the opposite way. On the other hand, in the African chamæleon and in the chamæleon-iguana strong light acts like low temperature, inducing the migration of the pigment-bodies to the skin, while dim light, or darkness, causes their withdrawal. In other words, while in the first case light and heat act in unison, in the second case their results are antagonistic.

These lizards are arboreal, hopping from bough to bough

like tree-frogs; and their changes in colour are very rapid in a state of nature.

Other tropical American lizards belonging to the family *Teiidae*, or *tejus*, and the genus *Ameiva*, also possess the power of changing colour, although apparently to a more limited extent; and in this case also the power seems to have been independently acquired. A fourth instance of a similar colour-change occurs in the Indian and Malay variable-lizard (*Calotes versicolor*); and since this species is a member of the family *Agamidae*, which has no near relationship with iguanas or *tejus*, the independent origin of the phenomenon may be considered as beyond doubt. These lizards, which in the Malay Peninsula are miscalled chamæleons by Europeans, are arboreal and pugnacious in their habits. The normal colour of the skin of the body is brownish, but when the lizard is feeding or excited this changes to pale yellow, while the head and neck become suffused with brilliant red. When the male is courting the female its hue becomes yellowish flesh-colour, with a conspicuous dark patch (which completely disappears when he is disturbed) on each of the throat-pouches.

As already mentioned, the coloration of a large number of snakes (including pythons and boas) appears to be of a protective nature, but only a few instances of special adaptation of this kind can claim notice. Among these, reference may be made to the occurrence of a green colour, to harmonise with their leafy environment, in several groups of those reptiles, as there appears to be evidence that this has been acquired independently in at least two of these groups. The American wood-snakes of the genus *Herpetodryas*, which belong to the typical subfamily of the great family of *Colubridæ*, are purely arboreal, and typically of a more or less uniformly olive-green tone of colour. The *sipo*, or Brazilian wood-snake (*H. carinatus*), for instance, is normally bright verditer or olive-green above, with a tinge of brown on the back, and greenish or bright yellow below. Curiously enough, however, probably owing to some difference in its habits—in the West Indies it becomes blackish or blackish brown above, with the under parts steel-grey. Nearly allied are the Old World and Australian tree-snakes of the genera *Dendrophis*, *Dendrelaphis* and *Chlorophis*, the latter of which is confined to Africa and takes its

name from the green colour characteristic of the group in general. Seeing that these snakes are nearly allied to the American *Herpetodryas*, it would be rash to affirm, despite their wide geographical separation, that their green livery has been independently acquired. Whatever doubt may exist in this case, it is practically certain that the arboreal Indian whip-snakes (*Dryophis*) and their American and Malagasy relatives of the genus *Philodryas* have developed their green colour apart from the members of the above-mentioned groups. For these snakes belong to a section of the *Colubridæ* in which the hind teeth in the upper jaw are grooved for carrying poison, whereas those of *Herpetodryas*, *Dendrophis*, etc., are solid ;—a difference implying a widely sundered ancestry. The long and slender bright green whip-snakes are almost impossible to detect when among the foliage of their native forests, and are even difficult to see when coiled among the branches of a small shrub in captivity. One species of viper (*Lachesis wagleri*) of the Malay countries is also bright grass-green in the young state, although later on the scales develop black edges, and in the adult condition the whole colour becomes blackish. This viper has a prehensile tail and feeds largely on birds, and is thus to a great extent arboreal. That the green colour in the young is protective and has been developed independently from that of all the colubrine tree-snakes is manifest; but why the creature should turn black in old age is a puzzle. Possibly the adult may lie more on the larger boughs than the young.

Many desert snakes present a remarkable protective resemblance to their surroundings. In no case is this more pronounced than in the horned viper (*Cerastes cornutus*) of North-eastern Africa and Arabia, which is sandy coloured, and in the day-time is in the habit of lying buried in the sand with only the eyes, nostrils and the horn-like processes on the head exposed, when it is practically invisible. The European rhinoceros-viper (*Vipera ammodytes*) presents a similar intimate resemblance to its desert surroundings. Although conspicuous when removed from its natural surroundings, the Cape puff-adder (*Bitis arietans*), with its yellowish or orange-brown ground-colour marked by chevron-shaped dark barrings, is almost invisible when on sandy and stony ground.

The last instance of protective coloration among snakes to



A



B



PROTECTIVE RESEMBLANCE IN REPTILES: BARK-GECKOS OF MADAGASCAR  
A.—THE LICHEN BARK-GECKO (*UROPLATES FIMBRIATUS LICHENI*)  
B.—THE COMMON BARK-GECKO (*UROPLATES FIMBRIATUS*)

which space admits of allusion occurs in the sea-snakes, forming the subfamily *Hydrophiinae* of the *Colubridæ*. As mentioned above, these snakes are noticeable for their compressed form, at least in the region of the tail. The majority are coloured almost exactly like mackerel; that is to say, the back is dark blue, from which descend bars of the same colour, separated by whitish interspaces of similar width; while the under surface is of the same silvery hue as these light interspaces. Obviously, as in the case of mackerel, the mottled blue of the upper parts harmonises with the rippled surface of the ocean and thus renders these snakes invisible from above; while their light under-parts when projected against the light of the sky render them equally inconspicuous to enemies from below. In one large species the dark upper surface is orange-brown instead of blue; the object of this departure from the normal type of coloration being at present unknown.

Tree-geckos in general, by their mottled hues of grey, white, and black, present a marked protective resemblance to the bark of forest trees; but the resemblance is carried to its highest degree in one variety of a Malagasy species known as the lichen bark-gecko, *Uroplates fimbriatus lichenium* (see Pl. V.). In this species, to which allusion will again be made, the upper surface is dotted with irregular whitish lichen-like markings upon a slate-coloured ground, so that the resemblance to lichen-coloured bark must be almost perfect when the creature is at rest with its flattened head, body, and tail closely pressed to the bough. Indeed the only part of the reptile that would appear in the least conspicuous would be its large and bloodshot eyes, and even these may perhaps assimilate in nature to the end of a recently broken twig. A few geckos, such as *Naultinus elegans* and *Thelsuma madagascariensis*, are coloured green to resemble foliage, the former being wholly of this tint, while the latter has the hind part of the back spotted with red.

As already mentioned, a number of ground-lizards are coloured slaty grey to harmonise with the prevailing hues of the rocks or soil on which they habitually dwell; but two instances may be cited where this protective coloration is specially noticeable. These are the two lizards commonly known under the names of the horned toad (*Phrynosoma cornutum*)

and the moloch (*Moloch horridus*). In the former the resemblance to dark-coloured soil is striking ; the skin being slaty grey with flecks of white and black. On the other hand, the moloch is coloured to harmonise with sandy soil containing brown pebbles or fragments of stone ; the ground-colour being buff, with a number of oval chocolate blotches. When half-buried in soil of the above description, the creature must be practically invisible ; the illusion being enhanced by the horn-like excrescences dotted over the head, body, and tail.

It is, however, by no means only such dull-coloured lizards that harmonise in hue with their surroundings. Few creatures are more brilliantly coloured than the eyed lizard (*Lacerta ocellata*) of Southern Europe, with its back of mingled flecks of gold and chocolate, the large bright blue "eyes" on the flanks and the brown head and tail. And yet there can be little doubt that these harlequin colours fade into a confused blue when this reptile is lurking among grass and other low herbage. Again, certain small snakes have their skins mottled with bright red and black ; a combination which although conspicuous in captured specimens, harmonises with soil composed of red sand mingled with dark pebbles. A similar type of coloration occurs in that American reptile known as the poisonous lizard, or gila monster (*Heloderma suspectum*), which is not uncommon in parts of Arizona and the neighbouring districts. If this reptile inhabit country with a soil of the above-mentioned description, its colouring must be of a protective nature, but such descriptions of its habitat as have come under my notice are silent on this point. On the other hand, the gila monster may present an example of "warning colour" ; that is to say, its bright colouring may be conspicuous and serve to warn enemies (by inherited experience) of its dangerous and poisonous nature.

In concluding this part of the subject, it may be pointed out that no reptiles display that peculiar protective arrangement of colouring so commonly developed in large mammals living in the open, which consists in having the under-parts light and the back dark, thus neutralising the effect of the shade cast by the body. And the explanation of this is not far to seek, for no existing reptiles have the body sufficiently elevated above the ground to make this type of coloration effective. It is not meant by this to assert that no reptiles

have light under-parts--they are in fact strongly marked in crocodiles and many snakes; but in these cases the lightness is due to the absence of any necessity for colour, these parts being concealed, and not to a special protective adaptation.

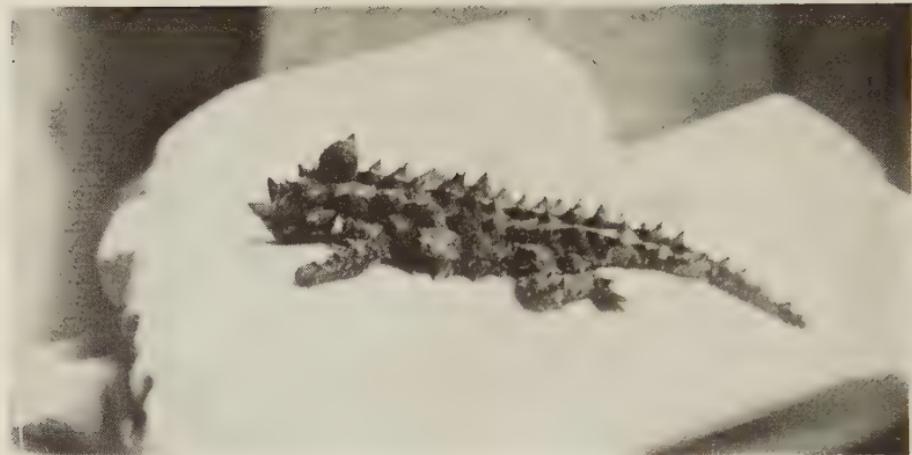
## CHAPTER VII

### ADAPTATIONS

ADAPTATIONS TO THE GENERAL CONDITIONS OF THE ENVIRONMENT: Terrestrial types. Arboreal types. Climbing types and effect on tail and feet. Running types. Bipedal types. Flying types. Swimming types. Sail-backed lizards. Limbless types. Burrowing types. Modification of the eye and ear. Dermal armour.

LIZARDS and crocodiles present what may be called the ordinary or typical form of body among reptiles—a form so familiar to all that nothing in the way of description is necessary. If, however, we examine a large series of reptiles in a museum (exclusive of those which have lost the limbs and assumed a snake-like form of body) we shall find that there are two distinct and well-marked modifications of this typical shape; the one pertaining to species which are terrestrial, and the other to such as are more or less completely arboreal in their mode of life. In all the purely terrestrial types, such as the common agama lizards, or stellions, of the Old World, for instance, the body is more or less markedly depressed, or flattened from above downwards, and much expanded laterally, so that the sides form comparatively sharp edges, while the limbs, which are generally short, thick, and powerful, are widely sundered from one another at their points of origin from the shoulders and haunches. Only a moment's reflection is required to show that such a construction of body and limbs is obviously the one best adapted to enable the owner to escape detection from enemies by squeezing itself as flatly and closely as possible upon the rock or sand upon which it happens to be resting, more especially when (as is almost invariably the case) its colour harmonises with that of its surroundings. The above-mentioned agamas, or stellions, for instance, are generally coloured some shade of mottled grey, brown, and blackish, so as to harmonise closely with the lichen-





MOLOCH LIZARD (*MOLOCH HORRIDUS*)



"HORNED TOAD" (*PHRYNOSOMA CORNUM*). TO SHOW DEPRESSED FORM OF BODY CHARACTERISTIC OF TERRESTRIAL TYPES OF LIZARDS



BEARDED LIZARD (*AMPHIBOLURUS BARBATUS*) OF AUSTRALIA

spotted rocks upon which they delight to bask in the sun. On the other hand, desert-haunting species are more usually of a sandy tint.

The extreme development of the depressed type of bodily form occurs in species which dwell on sandy or other soft soil, where the body can be closely pressed to the ground; this supreme development being found in species belonging to different family groups, thus demonstrating that its origin is dependent on adaptation to habits and environment and has nothing to do with zoological affinity. The best example of this is afforded by the two lizards respectively known as the moloch (*Moloch horridus*) of the deserts of Western and Southern Australia, and the American so-called "horned toad" (*Phrynosoma cornutum*), which inhabits similar situations in California. The former—the sole representative of its genus—belongs to the family *Agamidae*, while the latter, which is one out of about a dozen species of the same genus, is a member of the *Iguanidae*. Both have the body so depressed and flattened that it is nearly oval in shape; and in both, the head, body, and tail are covered with a number of short spines, evidently either for protection or to aid in concealment. In the moloch the colour is pale brown blotched with chocolate, while in the horned toad the prevailing tint is a mixture of yellow, brown, grey, and black. When squatting closely down in the sands of their native deserts, with which the colour of each harmonises, both these lizards must be difficult to detect; and when they are recognised, their prickly coats must render them difficult to pick up. Any non-scientific person seeing the two species side by side would almost certainly declare that they must be near relations; whereas their superficial resemblance to one another is a case of parallelism in development for the purpose of adaptation to their surroundings and consequent concealment from enemies (Pl. V.). The iguanas of the genus *Sceloporus* are also depressed terrestrial forms, quite unlike the arboreal compressed representatives of the family.

The spiny-tailed lizards (*Uromastix*) of the deserts of the Old World, which belong to the same family as the moloch, may be cited as other examples of the depressed type of body, although the depression is not carried to the same degree as in the instances described above. The spiny-tails are burrowing

lizards, which dwell in holes : these they invariably enter head-first, and the spiny tail consequently blocks the entrance in a most effectual manner to all would-be intruders—another instance of structural modification and adaptation for protective purposes. Crocodiles also offer an example of the depressed type of bodily form : but since these reptiles are to a great extent aquatic in their habits, the large and powerful tail has assumed a compressed form, so as to act as an oar or rudder in swimming ; its efficiency in this respect being increased by the elevation of the two edges of the upper surface into crests.

Although this depressed type of body is characteristic of purely terrestrial species, it would be a mistake to suppose that it is entirely confined to reptiles with such habits. On the contrary, it occurs in species habitually dwelling in trees, or frequenting walls or vertical rock-surfaces ; and, strictly speaking, therefore, this type of bodily contour may be met with among arboreal reptiles. It is, however, better to term species with this habit trunk-haunting or wall-haunting reptiles, for they are not arboreal in the sense in which an iguana or a chamaeleon is, that is to say, they do not dwell on the small branches and amid the leaves, but cling tightly to the bark of the trunk and larger boughs. The best examples of trunk-haunting reptiles with this depressed and expanded type of body are afforded by certain geckos, such as the Turkish gecko (*Hemidactylus turcicus*) and that variety of the Malagasy bark-gecko known as *Uroplates fimbriatus lichenium*. In the latter not only is the body greatly depressed and expanded, but the short and trowel-like tail is modified in the same manner ; and since, as already stated, the colouring accords in a marvellous degree with lichen-clad bark, the reptile must be practically invisible when clinging to the trunks it frequents. A further development of the depressed type of body is presented by the fringed gecko (*Ptychosoum homalocephalum*) of the Malay countries, in which the sides of the head, body, limbs, and tail are bordered by a thin membrane of considerable width. When clinging to a trunk, this membrane causes the outlines of the body to merge imperceptibly into the bark. If, however, it be true that it also serves as a parachute, this fringe must have a double function, namely as an aid in protection and as an organ of flight.

The arboreal type of bodily form, as presented in its

most characteristic development by iguanas (*Iguanidæ*) and chamæleons (*Chamæleontidæ*), is precisely the reverse of the terrestrial, that is to say, in place of being depressed, the body is compressed or flattened from side to side, so that the back and belly take the form of more or less sharp ridges, while the sides are extensive flattened surfaces. The tail partakes in a greater or less degree of the same modification; while the limbs, which are often of considerable length, must necessarily be separated from their fellows of the opposite side by a comparatively small space at the shoulders and haunches. Now it is clear that a reptile of this shape is admirably adapted to escape detection when standing on or clinging to a bough, as it may be easily mistaken for a broken branch, or, if coloured green, for a leaf or bunch of leaves. But chamæleons (and for aught I know, iguanas also) go one better than this, for when a stranger approaches the tree or shrub on which they may be resting, every one of them promptly moves to the opposite side of the branch, when its thin body is more or less completely eclipsed.

In the foregoing paragraph it has been mentioned that iguanas belong to one family of reptiles and chamæleons to another; from which we see that, like the depressed type, the compressed form has been independently developed in different groups. This, however, is by no means all, for we find among reptiles of the latter type an instance where species belonging to different families have acquired a superficial resemblance analogous to the one existing between the horned toad and the moloch lizard, and due to parallelism in adaptive development. The species between which this resemblance is most marked are the Indian chamæleon (*Chamæleo calcaratus*) on the one hand, and the chamæleon-lizard (*Ganocephalus chamæleontinus*) of the Malay countries on the other; the former typifying a family by itself, while the latter is a member of the *Agamidæ*. Both species display the same helmet-like form of the head, the laterally-compressed body, with a sharply keeled back, and the long tapering tail. The general colour of the two is likewise very similar. A certain difference is noticeable with regard to the spines on the back, which are more distinct in the chamæleon-lizard; but such a difference might be specific. Careful examination will show that the two reptiles

are really very different. The chamaeleon, for instance, has a granulated skin, while that of the chamaeleon-lizard is scaly. The latter species also lacks the telescopic eye of the chamaeleon, and the toes of each foot are not divided into opposing groups for grasping, nor is the tail prehensile. The chamaeleon's protrusile tongue has, moreover, no parallel in the lizard.

The resemblance between the two reptiles is, in fact, superficial, and doubtless correlated with their mode of life, both being purely arboreal creatures, of slow and sluggish habits, and feeding upon insects. The strange thing about the matter is that the resemblance should be as close as it is, seeing that chamaeleons are unknown in the countries east of the Bay of Bengal, and therefore that it cannot be due to mimicry of the one species by the other. The suggestion might arise that chamaeleons once inhabited the Malay countries, but there is no evidence of this. Moreover, the chamaeleon-lizard belongs to a rather large genus, some of the members of which inhabit India and Ceylon, where chamaeleons are found; but these species do not present anything like the same resemblance to chamaeleons as is shown by the chamaeleon-lizard and a few allied Malay species.

In connection with chamaeleons, it may be mentioned that these reptiles exhibit a modification in the structure of the feet unique in the class, although paralleled among birds by cuckoos and certain allied groups. Not only are the limbs of chamaeleons relatively long and slender, but two of the toes of each foot are permanently opposed to the other three; the first three toes in the fore-foot being opposed to the other two, while in the hind limb the inner division includes only the first and second toes, to which the other three are opposed. Additional aid in climbing is afforded by the prehensile tail, the tip of which can be curled downwards round a branch. Here, then, we have a function parallel to what exists among arboreal mammals, such as spider-monkeys, tree-porcupines, and opossums. The tail of the pythons and certain other snakes is also endowed with the power of prehension.

Geckos display a different modification of the toes for the purpose of enabling them to cling to walls, cliffs, and even ceilings, upon the latter of which they run back-downwards, like flies. This clinging function is effected by means of a number



A.—CHAMELEON LIZARD. B.—COMMON CHAMELEON  
TO SHOW SIMILARITY OF ARBOREAL FORMS IN WIDELY DIFFERENT TYPES



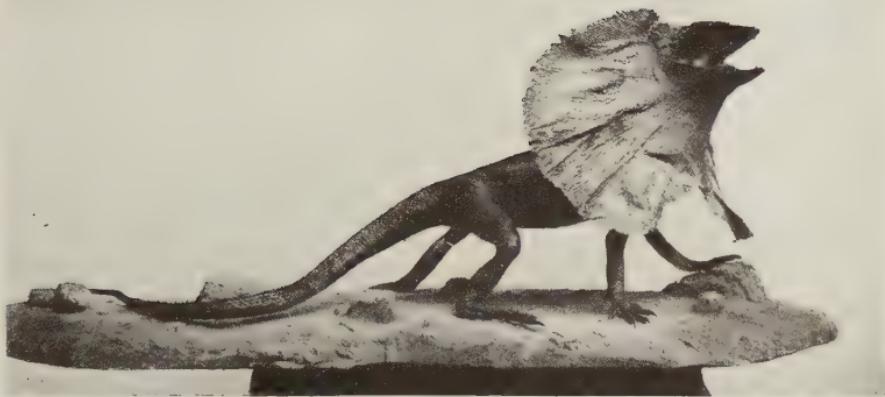
of spaces analogous in their action to suckers on the under side of the feet ; this surface on each toe being divided into such spaces by means of a series of transverse plates in the skin. When the foot is pressed upon a flat surface the soft, and yielding plates are squeezed flat and the air between them is consequently driven out. Elevation of the centre of the foot, which in some cases is webbed, consequently produces vacuums between the plates which act as suckers ; these vacuums being rendered more effectual than would otherwise be the case in the non-webbed species by the presence of a number of minute hairs on the edges of the plates. This sucker-like structure is present on the feet of many if not most geckos. In certain species, such as *Teratosaurus scincus*, of Persia and Turkestan, which have forsaken their climbing habits in favour of an existence on desert sands, the clinging apparatus has been lost or modified, so that the foot has reverted to a more normal type.

Another modification in connection with climbing is exhibited by the hind-feet of the iguanas, which attains its maximum development in the chamæleon-iguanas of the genus *Anolis*. In these reptiles the outermost, or fifth toe, is widely separated from the other four, which are elongated, and branches off at the root of the foot, so that its point of origin is higher up than that of the rest. In *Anolis* it looks quite distinct from the rest of the foot, and the whole foot is designed to form an efficient climbing instrument.

A few lizards, such as some of the American iguanas, and more especially the frilled lizard (*Chlamydosaurus kingi*) of Australia, whose bodies are formed on the compressed arboreal type, have deserted to a greater or less degree their original climbing habits, and taken to an existence on open sandy ground, where they run at times on the hind-legs, in the upright posture with the fore-limbs folded and hanging by the sides of the body ; the large throat-frill of the Australian species being on such occasions folded up like a badly-made umbrella. The frilled lizard cannot, however, maintain this running gait for any length of time ; and after a bit will either turn to bay at the foot of a tree, or run up the stem of the latter in the manner of a climbing lizard. The frilled lizard is a member of the *Agamidæ*. The same cursorial type occurs in certain smaller carnivorous representatives of the extinct dinosaurs,

such as *Compsognathus longipes*, from the Upper Jurassic lithographic limestone of Bavaria and *Ornithomimus altus* of the Cretaceous rocks of North America; and it has consequently been suggested that the frilled lizard has inherited the upright posture and running gait from dinosaurian ancestors. Nothing could be further from the truth, lizards being widely sundered from dinosaurs. The acquisition of the running habit in the frilled lizards, in certain iguanas, and in the carnivorous dinosaurs, on the contrary, is another instance of the independent development of similar adaptations. From a study of the skeleton of the fore-limb of the dinosaur *Ornithomimus* palaeontologists have come to the conclusion that the fore-foot was endowed with grasping and seizing power and consequently capable of acting as a hand; and since these reptiles, from the structure of their teeth, were evidently carnivorous, it has been suggested that they were in the habit of capturing on the wing the contemporary lizard-tailed birds, such as *Archæopteryx*, whose flight was probably slow, heavy, and low.

From the foregoing cursorial type, in which the upright posture was assumed either occasionally or permanently, the transition is easy to the giant herbivorous dinosaurs, such as *Iguanodon* of the European Wealden and a number of allied forms from the Upper Jurassic and Cretaceous strata of North America, in which the bipedal posture was habitual, although the gait was a walk, as is indicated by the impressions of the footsteps of these reptiles found in the sandstone of Hastings. The larger kinds of *iguanodon* (which take their name from a fancied resemblance between their teeth and those of modern iguanas) stood approximately twenty feet in height, and walked on their hind-limbs, with perhaps some support from the long and heavy tail, which probably acted as a counterpoise to the head and fore part of the body. Apparently the general shape of the trunk approximated more or less closely to the compressed arboreal type, although there may have been some greater degree of expansion in the region of the chest to allow of the free play of the fore-limbs which were evidently used as arms. The *iguanodons* and their allies were by no means the only large dinosaurs which habitually walked in the upright posture. The carnivorous *Megalosaurus*, for example, which when in this posture stood about a dozen feet in height,



AUSTRALIAN FRILLED LIZARD (*CHAMYDOSAURUS KINGI*) FROM  
A STUFFED SPECIMEN



SAME IN RUNNING POSITIONS  
PHOTOGRAPHED FROM LIFE



did so, although probably not so frequently or so persistently as the iguanodon.

The flying type is only properly developed in the extinct pterodactyles, or Ornithosauria. The so-called flying dragons (a name much more appropriate to the pterodactyles) constituting the genus *Draco* and belonging to the lizard family *Agamidæ*



FIG. 4.—Restoration of the Iguanodon.

have, however, acquired a kind of spurious flight, or rather are capable of taking flying leaps by means of a parachute-like expansion of the skin of the sides of the body. The depressed form of the body in the flying dragons shows that these lizards have been evolved from an ordinary arboreal member of the *Agamidæ* by an ultra-development of a membranous expansion of the skin of the sides of the body similar to that found in the fringed gecko. In the "dragons" the wing-like parachute of each side is supported by an outward extension of four or five

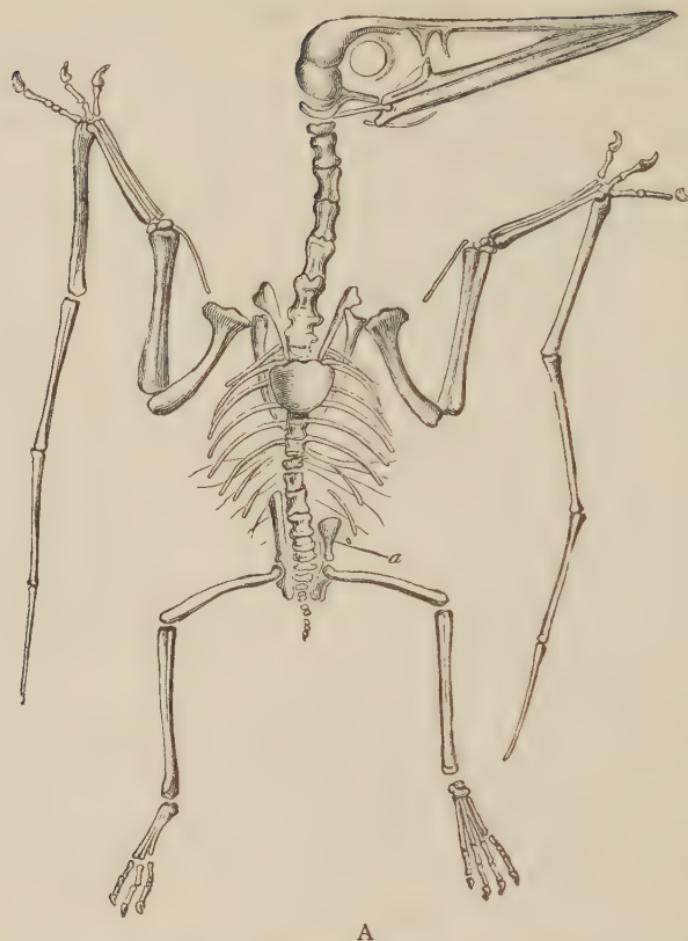
of the posterior ribs, and can be folded up fan-wise. The throat has a short fold in the middle and a pair of lateral flaps, but there is no expansion on the long whip-like tail, which is not brittle. These reptiles are confined to the Malay countries, where they simulate the gorgeous tropical flowers by their brightly coloured wings. Their powers of flight are but moderate; and there appears to be a considerable amount of misconception with regard to the position of the wings when at rest. For example, most books of popular natural history represent these lizards as resting on a branch with outspread wings. In the volume on reptiles in the *Cambridge Natural History* we read (p. 517) that "they do not fly by moving the wings, but when at rest upon a branch amidst the luxurious vegetation and in the immediate neighbourhood of gorgeously coloured flowers, which partly conceal them by their likeness, they greatly resemble butterflies, especially since they have the habit of opening and folding their pretty wings". A very different account must however be given as the result of observations on living specimens of *Draco volans* made by Dr. Paul Krefft<sup>1</sup> in Singapore. He holds that the brightly coloured parachute is hardly ever unfolded except for the purpose of flight; when the reptile is at rest, or running, the parachute is closely folded against the body, giving the impression of a lizard emaciated by starvation or recent oviposition, but showing no trace of brilliant coloration. The account of the colours of the male and female in life by Dr. Krefft agrees with that given by Captain Flower in the *Proceedings of the Zoological Society* for 1896. The latter observer states that these lizards when at rest on the trunk of a tree are almost invisible, owing to the dark mottled-brown tint, the bright colour of the wings showing only when they dart through the air.

In the case of the fringed gecko (*Ptychozoum homalocephalum*), which is likewise a Malay reptile, the membranous expansions are said to serve the purpose of a parachute but this requires confirmation.

As already mentioned, three tree-snakes from Borneo are stated by the natives (and native testimony has generally a foundation of truth) to possess the power of taking flying leaps from the boughs of trees to the ground (see p. 34).

<sup>1</sup> *Zoologischer Garten*, August, 1904.

In the extinct pterodactyles (Ornithosauria) the whole organisation, both external and internal, is modified for the purpose of true flight in the air, and there are consequently many superficial resemblances to birds. Nevertheless, all these are adaptive, and not indicative of avian affinities; these reptiles having probably branched off from the common stock of dinosaurs and crocodiles independently of birds. The head is very bird-like, having a long beak, which was probably in all cases sheathed with horn, although in the earlier forms (as in primitive birds) the jaws were furnished with a series of pointed teeth. On the other hand, the wings were membranous and more like those of bats, being attached not only to the greatly lengthened fore-limbs, but also to the sides of the body and the hind-legs, as well as to the base or the whole of the tail. In the fore-limb there were only four digits, the one corresponding to the thumb being absent. Of the four digits the three inner were short and carried sharp claws, probably employed in clinging to rocks or possibly branches; the outermost digit, or the one corresponding to the human little finger, was, on the contrary, enormously elongated, and alone carried the wing. In the earlier long-tailed forms the tip of the tail was furnished with a racket-shaped membranous expansion, which probably served the purpose of a rudder in flight. Apparently, however, it was found better to entrust the steering to the wings alone, for in the later and specialised forms, notably those without teeth, the tail is rudimentary. The largest species of which the skeleton has been discovered is *Pteranodon longiceps*, of the upper Cretaceous rocks of Kansas the expanse of wing being no less than 14 feet, or greater than in the largest albatross, while the head, which was extended much behind the line of the backbone, was about a yard in length. In *P. ingens* of the same formation the expanse was fully 22 feet. The pterodactyles of this genus are remarkable for the fact that the "white," or sclerotic, of the eye was furnished with a ring of bony plates similar to that found in the eyes of birds and in those of the extinct ichthyosaurs, as well as in certain extinct marine crocodiles (*Geosauridæ*); such a structure being unknown in the smaller and earlier members of the order. Evidently, this bony sclerotic ring has



A



B

FIG. 5.—A, Skeleton of a Short-tailed Pterodactyle (*Pterodactylus spectabilis*) from the Upper Jurassic of Bavaria. B, Restoration of a Long-tailed Pterodactyle (*Rhamphorhynchus phyllurus*) from the same formation (from *Guide to Fossil Reptiles, etc., in the British Museum—Natural History*).

been independently acquired in the four groups. In the ichthyosaurs and pelagic crocodiles its function may have been to aid in resisting the pressure of the water at great depths ; but what may be its use in birds and pterodactyles is not easy to determine. In the case of birds it was at one time supposed that the function of this arrangement was for the purpose of altering the degree of convexity of the cornea during rapid ascent or descent in the air, but objections have been urged against this view ; and, so far as it goes, the occurrence of the same structure in pterodactyles tends to support this objection, since it is scarcely likely that these reptiles were capable of soaring to great heights in the air. When on the ground, or during repose, pterodactyles certainly folded their wings, although the precise manner in which they were then carried is uncertain. From the fact that in the fine lithographic limestone of Bavaria, where complete skeletons and occasionally the impressions of the wing-membranes are found, no traces of scales, hair, or feathers have been detected, it is practically certain that pterodactyles had naked skins. If we seek a reason why the specialised pterodactyles discarded teeth in favour of a smooth horny beak, it may be observed that all members of the group probably fed upon fish. Now at first sight it might appear that toothed jaws were better adapted for holding slippery prey than is a toothless horny beak ; but it has to be borne in mind that although toothed jaws would ensure the retention of every fish captured, yet they would prove a hindrance to its being quickly and easily swallowed. Possibly, indeed, it may have been necessary for a toothed bird or pterodactyle to resort to the shore before being able to devour its prey ; and if this were were the case, we have an explanation why birds and pterodactyles became toothless. That pterodactyles habitually frequented the sea-shore, if not the open sea, is demonstrated by the occurrence of their remains in marine strata side by side with those of ichthyosaurs, plesiosaurs, and mail-clad fishes.

Many reptiles of the normal type, such as crocodiles and ordinary snakes, are excellent swimmers, and some (apart from sea-snakes) will venture considerable distances out to sea. In all of these, however, no special modification, either external

or internal, beyond the webbing of the feet in crocodiles and certain peculiarities in connection with the breathing apparatus, has been evolved to adapt them to an aquatic life. On the other hand, there are several distinct groups of reptiles in which some or all of the species have been profoundly modified in accordance with the needs of a pelagic mode of existence. Such are the sea-crocodiles, *Geosaurus*, *Dacosaurus*, and *Metriorynchus*, constituting the family *Geosauridae* of the order Crocodilia; the ichthyosaurs or fish-lizards forming the order Ichthyopterygia; the plesiosaurs and pliosaurs, representing the order Sauropterygia; the mosasaurs, or "sea-serpents" (*Mosasaurus*, etc.) which form a separate suborder of the Squamata; and the dolichosaurs (Dolichosauria), which constitute a second subordinal group of the latter order. The turtles, again, represent a specialised group of the order Chelonia modified for an aquatic life. In the latter case the modification has not been carried to the same extent as in the other groups, for these reptiles habitually resort to the shore at certain seasons, whereas some of the former were as purely pelagic as are whales and porpoises at the present day, *Ophthalmosaurus* being the most so among the ichthyosaurs. It is curious that all the above-mentioned groups of pelagic reptiles are extinct at the present day, their place (unless the "sea-serpent" be a reality) having been taken by the Cetacea, which have ousted them in the struggle for existence. Further, each of these extinct groups has been (like the Cetacea) independently evolved from terrestrial forms although it is not in every instance possible to point to the ancestral type. Had they been derived from more primitive groups of marine vertebrates, such as fishes, it is evident that, like the latter, they would have breathed the air dissolved in water by means of gills, instead of being compelled to rise (like whales) at intervals to empty and refill their lungs with atmospheric air. In every case one pair of limbs has been converted into paddles, or flippers, with digits united by a common integument; but the structure of the skeleton of these paddles is subject to great variation in the different groups; this being alone sufficient to demonstrate the independent origin of the latter. Moreover, apart from the turtles, a more or less whale-like or eel-like type of body has been assumed by the members of these pelagic groups.

The pelagic crocodiles, for which the name *Thalattosuchia* has been suggested, are typified by the genus *Geosaurus* of the upper Jurassic strata, closely allied to which is the much larger *Dacosaurus* of the English Kimeridge Clay. *Geosaurus* ("land-lizard") is an unfortunate title for a pelagic reptile, but less confusion will be caused by its retention than by proposing a more appropriate designation. These crocodiles, which are presumed to have branched off at an early date from the primitive terrestrial stock which subsequently gave rise to the modern representatives of the order, discarded the armour of bony plates overlain by horny shields which forms such a distinctive feature of land crocodiles, as being ill-suited to a marine existence, and acquired instead a smooth skin like a whale. In form the body was much elongated, so as to resemble that of a conger-eel, and the long tail probably terminated in a fin, while there may have been fin-like expansions on the line of the back. The front limbs, which were smaller than the hind pair, were alone modified into perfect paddles, and were probably the chief propellers; the hind-limbs being apparently held close to the sides of the body. The jaws were long, and the eyes, as already mentioned, furnished with a ring of bony plates in the sclerotic, probably for the purpose of resisting the extra pressure of the water when diving. *Metriorhynchus* of the Oxford and Kimeridge Clays was a nearly allied type.

Very different in appearance to the pelagic crocodiles were the ichthyosaurs, or fish-lizards (*Ichthyopterygia*), of which the rude outline of the external form has been preserved in some of the fine-grained clays of the Lias. In these reptiles the general contour was exceedingly fish-like or whale-like: the body being fusiform, and the tail terminating in a large fin, or "flukes," while there was also a back-fin. Unlike that of whales, the tail was, however, vertical, with the backbone continued into the lower lobe. Of the two pairs of paddles, the front ones were much the larger, and doubtless the more important in swimming. As in the pelagic crocodiles, the eye was furnished with a ring of sclerotic plates, which may be taken as an indication that some of these reptiles, which attained a length of fully thirty feet, were in the habit of diving to considerable depths in the ocean. Ichthyosaurs present a curious parallelism to whales in

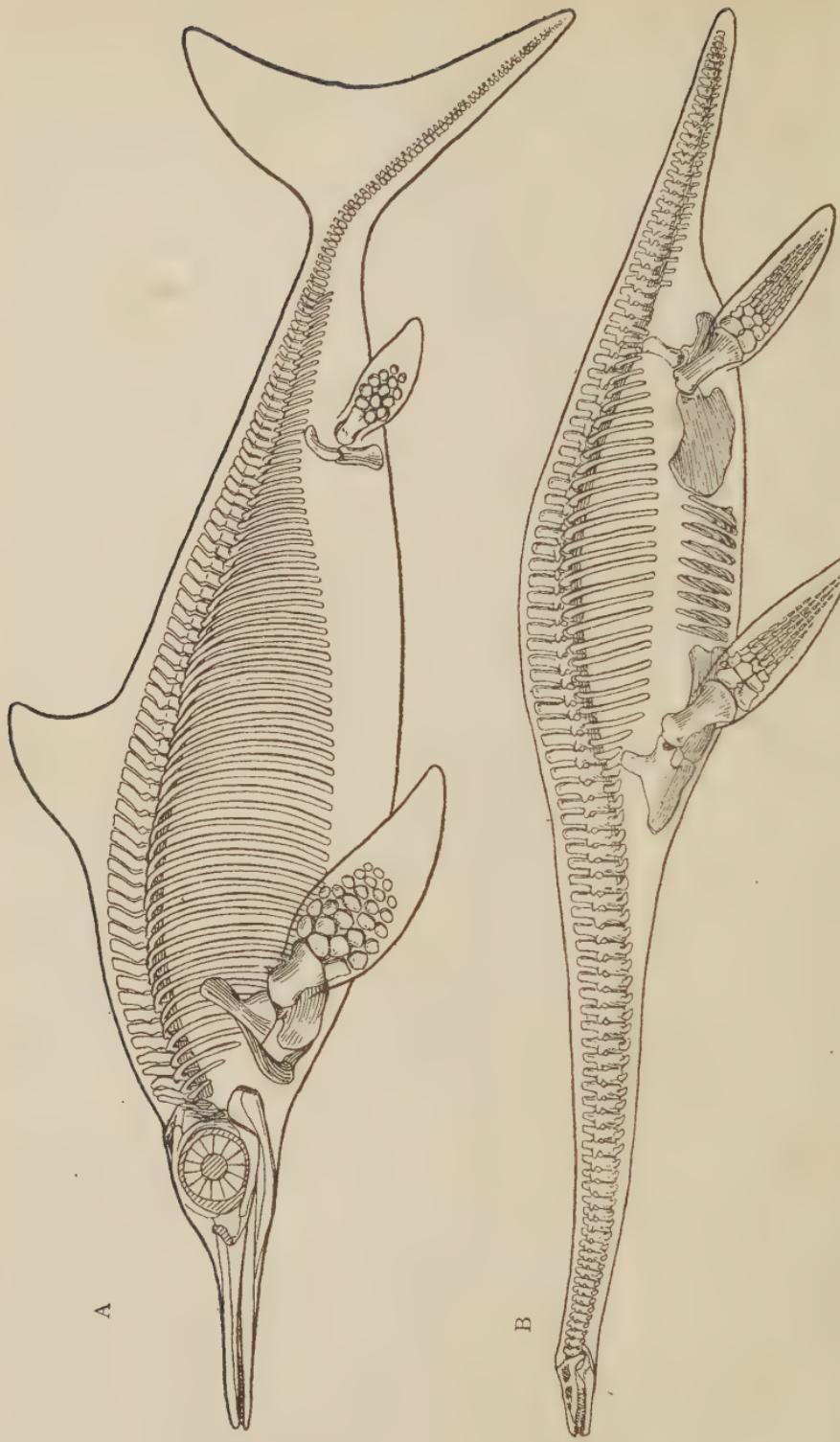


FIG. 6.—A, Skeleton with outline of body of an Ichthyosaur. B, Skeleton with outline of body of a Plesiosaur. After Dr. C. W. Andrews.

that some of the later and more specialised forms were without teeth. Whether, however, they developed in compensation any structure comparable to whalebone, or baleen, we shall never know.

Plesiosaurs (order Sauropterygia) were very different-looking reptiles to ichthyosaurs externally, from which they also display marked divergence in the structure of the skeleton, indicating their derivation from a totally distinct ancestral stock. In the more typical forms, such as *Plesiosaurus* and *Thaumatosaurus* of the Lias, the body was somewhat turtle-shaped, the tail comparatively short and pointed, the neck very long and slender, the head relatively small, and both pairs of paddles long and narrow. Apparently there was no fin on either the back or the tail, and the eyes lacked a bony sclerotic ring. Possibly the latter feature indicates that the plesiosaurs were not in the habit of descending to such depths as some of the ichthyosaurs—a suggestion supported by the shape of the former, which does not seem to be one well adapted for diving. Not improbably they swam with the whole neck and body partially above the surface and frequented the neighbourhood of the shore. Owing to the shortness of the tail and the length of the paddles, their mode of swimming must have been quite different to that of the ichthyosaurs, the paddles being the sole propelling instruments. Some of the species equalled the largest ichthyosaurs in point of size. Much the same contour of head, neck, and body is displayed by the plesiosaurs of the Middle and Upper Jurassic and Cretaceous strata, such as *Muraenosaurus* and *Cimoliosaurus*, although in some cases the neck was relatively longer than in their Liassic predecessors. On the other hand, the gigantic pliosaurs (*Pliosaurus*) of the Oxford and Kimeridge Clays developed an immense and ponderous head, which necessarily entailed for its support a short and thick neck. These are more adapted for a pelagic life, although not to the same degree as the whale-like *Ophthalmosaurus* among the ichthyosaurs. The earliest reptiles that have been referred to the Sauropterygia are small Triassic species (*Neusticosaurus*) of only about a foot in length, in which the limbs appear to have formed less perfect paddles, and whose habits were probably subaquatic and fresh-water. With the close of the Cretaceous epoch, the plesiosaurs, like

their contemporaries the ichthyosaurs, appear to have more or less completely died out, although a few may have survived into the early part of the succeeding Tertiary period.

Not till the Upper Cretaceous did the great snake-like swimming marine reptiles which may be popularly called sea-serpents or mosasaurs but are technically termed Pythonomorpha, make their appearance on the scene. They form a subordinal group of the order Squamata of equal rank with the Lacertilia and Ophidia. The body was greatly elongated, with paddles widely sundered from one another, and there does not appear to have been a back-fin. As in snakes, the two halves of the lower jaw were movably united by ligament in front; there were no bony plates in the eye; and the skin was probably naked. The typical *Mosasaurus* (so called from the Latin name of the river Meuse, on the banks of which its remains were first discovered) had a skull of about four feet long, and attained a total length of something like five-and-twenty feet. The giant of the group—a real “sea-serpent”—seems, however, to have been a New Zealand representative of the genus *Liodon*, whose length has been estimated at no less than 100 feet. The Pythonomorpha may have been derived from lizards more or less nearly related to the monitors (*Varanidae*), some of the extinct representatives of which attained hugh dimensions.

Yet another extinct group of marine reptiles allied to the lizards is represented by the Dolichosauria, which form a second suborder of Squamata, characterised by the paddle-like form of the limbs being less pronounced than in the Pythonomorpha and by the bony union of the two halves of the lower jaw. These reptiles likewise came into existence only with the Chalk and disappeared with the Tertiary. The typical *Dolichosaurus* of the English Chalk was a reptile of about a yard in length, as was also *Acteosaurus* of Istria, in which the front-paddles are known to have been decidedly smaller than the hind-pair, while the tail was long.

The sea-snakes, forming the subfamily *Hydrophiinae* of the *Colubridae*, afford an instance of what may be called a double adaptive modification, for they are evidently descended from ordinary snakes, which have been evolved from a four-limbed group by the excessive elongation of the body and the loss of

the limbs for a gliding mode of motion. The sea-snakes have been further modified for a pelagic existence by the lateral compression of either the tail alone or the whole body and tail, and the reduction in the size of the scales on the under surface, which are frequently not larger than those on the upper parts.

Sea-snakes, of which there are several genera, such as *Hydrophis* and *Enhydrina*, with somewhere about fifty species, are mainly pelagic, most of them dying if kept for any length of time out of water; they even breed at sea, and for this purpose are all viviparous. The largest species attain a length of about six feet. All are highly poisonous, and feed upon fishes which they kill by means of their poison-fangs. A single species, *Distira semperi*, is found in the land-locked fresh-water Lake Taal in the island of Luzon in the Philippines; this species, presenting an exact analogy with the seals which inhabit Lake Baikal, in Central Asia. The marine forms are confined to the tropical seas, in which they are met with from the Persian Gulf to Central America. In Samoa they are eaten by the natives.

It should be mentioned that, in addition to the true sea-snakes, a species of a very different group of serpents, namely *Hypsirhina hydrinus*, of Siam and the Malay Peninsula, has taken to a marine existence, and has consequently acquired a form of body recalling that of the *Hydrophiinae*. It has much the same habits as the members of the latter, swimming far out to sea in search of the fishes which form its prey. Here we have an instance of the assumption of the bodily form and habits distinctive of a particular group by a member of a totally different section.

The marine turtles, of which there are two distinct families, namely the *Chelonidæ* represented by the true turtles, such as the green turtle (*Chelone mydas*) and the logger-head (*Thalassochelys caretta*), and the *Dermochelyidæ*, which includes only the luth or leathery turtle (*Dermochelys coriacea*) afford a still more marked instance of a double adaptive modification. The true turtles are undoubtedly descended from terrestrial chelonians, which have themselves been specially modified by the development of the characteristic shell from some unknown type of more ordinary reptiles; the intermediate type between turtles and tortoises being represented by certain extinct Jurassic

chelonians, such as *Thalassemys*. The turtles themselves show their special adaptation to a pelagic existence by the heart-shaped form and marked depression of the shell (this being the form best adapted for swimming), and by the conversion of the limbs into complete paddles, which, however, retain some of the claws, and are thus suited also for progression, although of a poor kind, on land. The fore-limbs are much larger than the hind-pair, and form the main instruments in propelling the



FIG. 7.—A, The Luth or Leathery Turtle, to show the paddle-like limbs and shell covered with leathery skin. B, Portion of bony shell showing mosaic-like structure.

body through the water. A very similar modification in form is presented by the leathery turtle or luth, in which, however, the shell is composed of a mosaic-like pavement of small bones lying loosely on the ribs, instead of a comparatively small number of larger bones firmly welded to the latter; the fore-paddle being also relatively longer. There is a difference of opinion among naturalists as to the relationships between the *Chelonidae* and the *Dermochelyidae*. By some authorities each group is believed to have been independently evolved from terrestrial or fresh-water tortoises, while others regard the luth and its extinct allies as specialised, and as regards the structure of the shell de-

generate, derivatives from the ancestors of the true turtles. If the former view be true, we have evidence of another structural adaptation to an aquatic life; for in both the *Chelonidae* and the *Dermochelyidae* the temporal region of the skull, unlike that of ordinary chelonians, is roofed over with bone, and if this has been developed independently in two pelagic groups, it must evidently be an aquatic adaptation. In any case, the latter conclusion is supported by the fact that a similar structure, although in a minor degree, is developed in the fresh-water chelonians known as snappers which constitute the family *Chelydridae*. In the last-named family, as well as in the fluviatile soft-tortoises (*Trionychidae*), the adaptation to an aquatic existence has not been carried sufficiently far to have modified the limbs into paddles; the members of both groups spending much of their time on land.

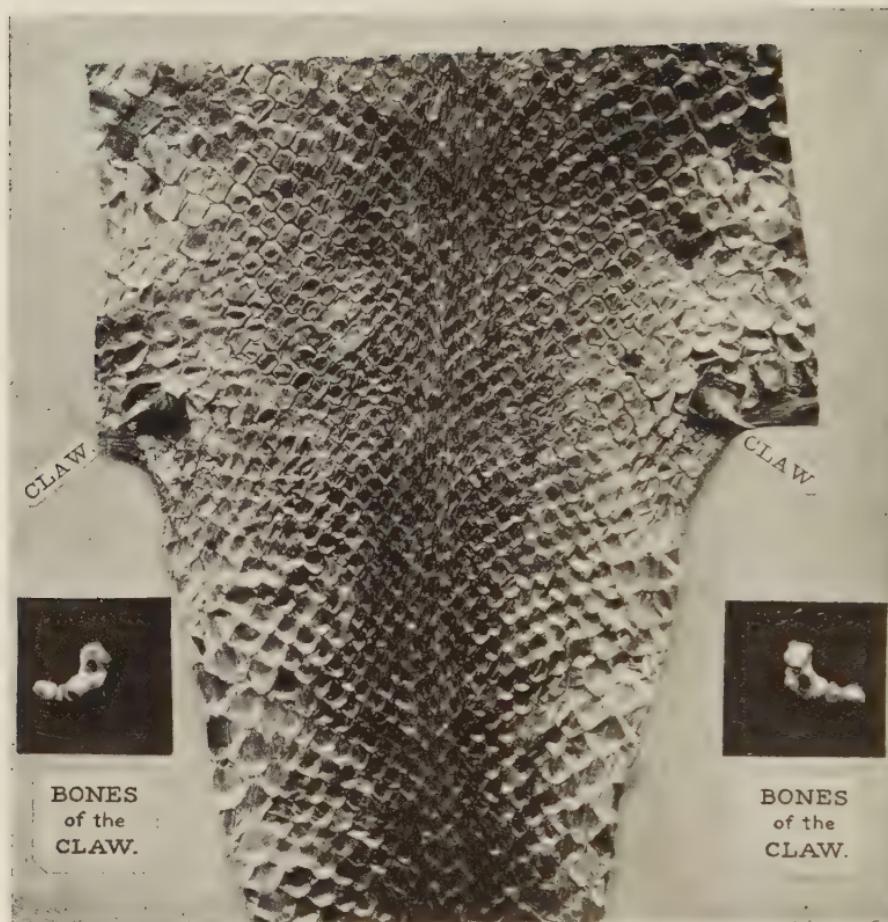
In this place may be mentioned a curious modification occurring in some recent and in a group of extinct reptiles, which has evidently been independently acquired, and would seem to be adaptive, and perhaps connected with aquatic habits, although this is by no means certain. Moreover, the modification in question is not structurally identical in the two cases, being formed in the one entirely by dermal tissues while in the other the vertebral column is involved. One of the most remarkable of the American *Iguanidae* is the basilisk, or sail-backed iguana (*Basiliscus americanus*), in the males of which the back and the middle line of the upper surface of the tail carry a tall sail-like crest, supported by flexible rods, and fully equal in height to the depth of the body. These basilisks, like other iguanas, habitually live in trees, preferring, however, those which overhang water, into which, when alarmed, they throw themselves, and swim away with strong strokes of the limbs. From the fact of the crest in all the species (for there are several) being confined to the males, it has been urged that it has nothing to do with swimming; but until we know definitely whether the males are better swimmers and more prone to take to the water than the females, this conclusion cannot be accepted without hesitation. Possibly the structure in question may be merely an ornamental appendage of the male sex, like the large comb of a cock. Be this as it may, it is dif-

ficult to accept the latter explanation in the case of the extinct group referred to above. In these reptiles, which occur in the Permian strata of North America and constitute the family *Clepsydropsidæ* of the order Pelycosauria, the spines of the vertebræ of the back are elongated to a height of about two feet, whereas the bodies of the vertebræ themselves are not more than an inch in diameter. In some cases, as in *Naosaurus claviger*, these upright vertical spines carried horizontal projections like yardarms. In life it is difficult to suppose that these remarkable "masts" could have had any other function than to support a large sail-like or fin-like membranous expansion. Now such a sail-like structure, so far as we can see, would have been a monstrous inconvenience and impediment to a terrestrial animal ; and it can therefore only be concluded that *Naosaurus* and *Clepsydrops* were, to a great extent at any rate, aquatic, and that the sail-like structure had some connection with the action of swimming. Possibly it may have acted as a real sail, as is said to be the case with the huge back-fin of the existing swordfishes of the genus *Histiophorus*.

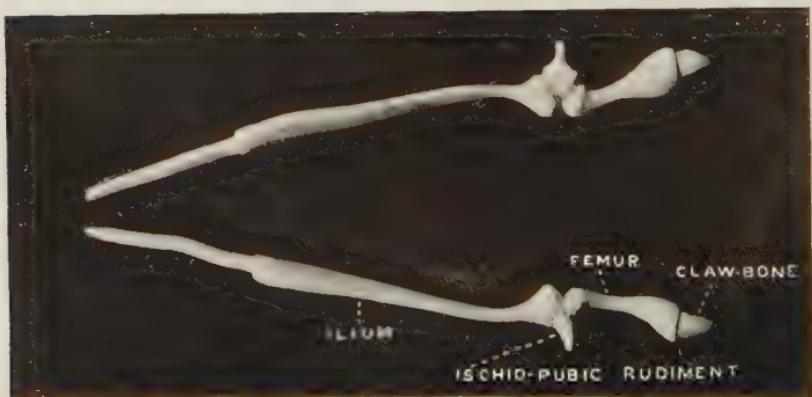
A very large number of reptiles, dating from the Cretaceous onwards but apparently attaining their maximum at the present day, have acquired an extremely elongated, slender, and more or less nearly cylindrical form of body, with the partial or complete loss of all external traces of both pairs of limbs. In most cases this snake-like type of body has apparently been acquired in the first instance as an adaptation to a gliding mode of movement on the ground, a burrowing, arboreal, or aquatic mode of life having apparently been sometimes developed from this original gliding type. In other cases, however, as in the skinks, the adaptation has been directly developed for a burrowing existence.

Adaptation to the gliding or limbless burrowing type has been independently acquired in at least six totally distinct groups of reptiles. Firstly, we have the entire group of snakes, constituting the suborder Ophidia of the order Squamata, and represented by several families ; secondly, the family *Anguidæ*, or snake-lizards, as represented by the English slow-worm or blind-worm (*Anguis fragilis*), and the much larger glass-snake or scheltopusik (*Ophisaurus apus*) of the Continent ; thirdly, certain types allied to the *Anguidæ* ; fourthly, the am-





PART OF THE SKIN OF AN AFRICAN PYTHON (*PYTHON SEBAC*).  
SHOWING EXTERNAL VESTIGES OF THE HIND-LIMBS



COMPLETE BONES OF THE HIND LIMB-GIRDLE IN SAME SPECIES

phisbænas (*Amphisbænidæ*) ; fifthly, the Australian scale-foots (*Pygopodidæ*) ; and, sixthly, certain skinks, more especially some members of the genera *Chalcides* and *Lygosoma* in the family *Scincidæ*, together with a few other degraded forms which have been made the types of families. All these groups except the first are members of the suborder *Lacertilia*, which forms a division of the *Squamata* of the same rank as the *Ophidia*.

Snakes, as being the typical, and at the same time the most numerous, "gliders," may be discussed first. The shape of these reptiles is familiar to all. A special feature is the presence of large transverse scales, or shields, extending right across the lower surface of the body, but on the tail frequently divided into a double series. Each scale corresponds to a pair of ribs; and in gliding a snake advances the fore-part of its body, when the scales on the lower surface are partially erected and take hold of the ground or other surface in such a manner that the rest of the body may be drawn forwards. As the ribs are the active agents in this peculiar mode of progression, snakes may be appropriately called rib-walkers. It should be added that the movements of a snake on the ground are, with the exception of the head and neck, confined to oscillations in a horizontal plane. Certain snakes display unmistakable evidence of their derivation from reptiles of a more ordinary type by the retention, either externally or internally, or both together, of vestiges of the hind-limbs. In the pythons and boas (*Boidæ*) such external vestiges take the form of a pair of small scale-like or spur-like structures in the neighbourhood of the vent. In the African *Python sebæ* these vestiges form distinct claws; but in specimens of *P. molurus* twenty feet in length they are scarcely visible. Somewhat similar but smaller vestiges also occur in the coral-snake (*Ilysia scytale*) and the other members of the family *Ilysiidæ*. The internal vestiges, which occur both in the *Boidæ* and the burrowing *Glauconiidæ*, take the form of remnants of the pelvis and occasionally also of the femur or thigh-bone. In no instance does any trace of the fore-limbs persist, thus showing that these were the first to disappear. Many snakes, such the pythons and tree-snakes (*Dendrophis*) have taken to an arboreal existence. Another group, the sea-snakes, or *Hydrophiinæ*, has, as already mentioned, taken to a pelagic

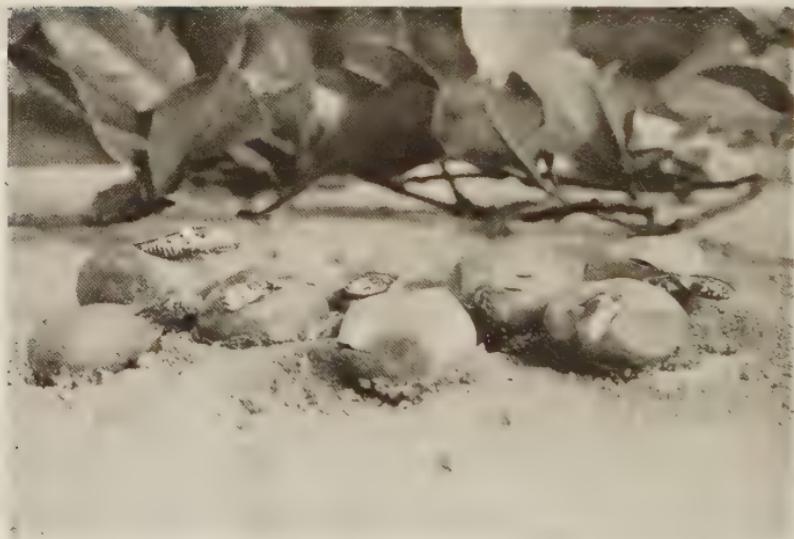
existence, with the assumption of a compressed form of body or tail, and the loss of the enlarged scales on the under surface, which would manifestly be an inconvenience in swimming. These large ventral scales have also completely or partially disappeared in four families of which the members lived a wholly or partially subterranean life; the disappearance being correlated with completely burrowing habits. These four families are the blind snakes, or *Typhlopidae*, the ground-snakes, or *Glauconiidae*, the coral-snakes, or *Ilysiidae*, and the shield-tails or *Uropeltidae*; the latter taking their name from the oblique truncation of the tail, the shield-like terminal surface of which is said to perform the work of excavating the burrow. These various burrowing snakes are evidently degraded types which took to a burrowing mode of life at an early stage of the evolution of the Ophidia; this early branching-off from the main stock being demonstrated by the retention in some of them of rudiments of the pelvis. Probably the four families have been modified for the same mode of existence independently of one another. The *Typhlopidae* have at the present day a wide geographical distribution, although they are unknown in New Zealand, and at one time were probably cosmopolitan. Although they are called blind snakes, they have not really lost their eyes, which are, however, hidden by folds of skin. They are confined to tropical countries, and feed largely upon earth-worms.

In these burrowing snakes the head, body, and tail are generally cylindrical, in adaptation to their particular mode of life; and in many of the more typical snakes, such as pythons and the grass-snakes, there is a marked tendency towards this cylindrical form in the body, although its under surface is more or less flattened for the purpose of gliding on the ground. In certain snakes dwelling in desert sands, more especially many members of the viper group, such as the puff-adder (*Bitis arietans*) and the horned viper (*Cerastes cornutus*), the head and body are much depressed and flattened, the head being remarkably broad and flat. This depressed form is obviously for the purpose of enabling these reptiles to lie close on the sand, and thus the more easily to escape detection; and affords an exact parallel to the acquisition of a similar depressed type by sand-haunting lizards like *Phrynosoma* and





GLASS-SNAKE TO ILLUSTRATE THE  
ASSUMPTION BY LIZARDS OF THE  
GLIDING TYPE OF CONFORMATION  
CHARACTERISTIC OF SNAKES



RING-SNAKES HATCHING

*Moloch.* On the other hand, in some of the tree-snakes, such as those of the Old World genus *Dendrophis*, the body tends to the compressed type, thus displaying another adaptive parallel to lizards, in which, as we have seen, the arboreal species have a compressed form of body. The tree-snakes of the genus above-mentioned have, however, a special modification for climbing, this taking the form of a pair of keels flanked by notches on the scales of the under side of the body ; by the additional hold on the bark thus afforded these snakes are able to glide along branches in a nearly straight line, instead of having to pursue the usual sinuous course.

Complete assumption of the gliding type of bodily contour occurs in the more typical members of the snake-lizards of the family *Anguidæ*. Indeed the slow-worm (*Anguis fragilis*) and the glass-snake or scheltopusik (*Ophisaurus apus*) are universally regarded in popular estimation as true snakes, from which they may be at once distinguished by the presence of movable eyelids, as well as by the brittle tail, which can readily be snapped in twain. The mention of eyelids calls for the remark that the name "blind-worm" is a misnomer, the creature having perfectly well-developed and functional, although small, eyes. Traces of the shoulder and pelvic girdles are always met with in the family, but the limbs may be either fully developed or entirely aborted. The slow-worm, in which the body is entirely covered with small cylindrical scales like those of the blind-snakes, exhibits the extreme degree of specialisation, the limbs being entirely aborted. On the other hand, in the glass-snake, in which the body is greatly elongated although the head is that of a typical lizard, there are vestiges of the hind-limbs in the form of a pair of small, half-concealed spines on each side of the vent. When, however, we come to the species of the tropical American genus *Gerrhonotus* we find both pairs of limbs fully developed, each foot having five complete toes. We thus have circumstantial evidence of the loss of the limbs in certain species within the limits of the family, although it is not to be supposed that *Gerrhonotus* represents the actual type from which the snake-like forms have been evolved. In summer both slow-worms and glass-snakes live chiefly among grass and leaves, although in autumn many individuals of the former make burrows in which they pass the winter.

On the other hand, the amphisbænas (*Amphisbænidæ*), so called from the similarity of the head to the tail and the possession of the power of going equally well either backwards or forwards, are purely burrowing lizards, with a remarkably worm-like appearance, the body being divided into numerous rings or segments, each divided into a number of squares representing aborted scales; functional scales being restricted to the head, with the exception of the members of the genus *Chirotes*, in which there are short four-clawed front-limbs, amphisbænas are completely worm-like lizards, although they retain vestiges of the bones of the shoulder and pelvic girdles, those of the former being the more reduced. Amphisbænas, which frequently infest ants' nests and manure-heaps in tropical countries, progress in a different manner to snakes and other snake-like lizards, the body being thrown into vertical instead of horizontal undulations; this alone being sufficient to demonstrate their independent origin from some extinct four-limbed stock. The numerous species of the typical genus *Amphisbæna* are restricted to tropical America and Africa; but *Blanus cinereus*, a pinkish, grey-flecked species, is common to Spain, Portugal and Morocco.

As already stated, in all these reptiles the eye is more or less degenerate; and in describing the structure of this organ in the amphisbænan known as *Rhineura florida*, Professor C. H. Eigenmann refers to the occurrence of a fossil representative of the same genus in the Miocene of Dakota. Nothing is known with regard to the eyes of the extinct form, but from the fact that all the living members of the group are blind, it seems practically certain that the degeneration of the eyes took place before the differentiation of the existing genera, in other words, at least as early as the Lower Miocene. In the existing form not only is the eye invisible externally, but there is no indication of the aperture by which it formerly opened on the surface.

Yet another independently evolved group of snake-like lizards is represented by the half-score or dozen species of the Australasian family *Pygopodidæ*, in which vestiges of the hind-limbs are retained in the form of scaly fin-like flaps; these frequently showing distinct remnants of the five toes. In *Pygopus* itself, as typified by *P. lepidopus*, the limb-flaps are of

considerable size ; but in *Lialis burtoni* they are reduced to minute almost imperceptible filaments. It will not fail to be noticed that the *Pygopodidae* differ from *Chirotus*, the one genus of the *Amphisbaenidae* with vestigial limbs, in the retention of remnants of the hind instead of the front pair. Although nothing definite appears to have been ascertained with regard to the habits of these "scale-footed" lizards, it may be inferred from this difference that they are not burrowing.

The last group that has to be noticed from the present point of view is that of the skink-lizards (*Scincidae*) and certain allied types. A large number of skinks are lizards of ordinary form, although they often show a marked tendency to elongation of the body. In certain species of the genera *Chalcides* and *Lygosoma*, which habitually dwell in sandy situations and have burrowing habits, this elongation of the body becomes especially noticeable, and is accompanied by a tendency to the loss of the limbs. These skinks seem, indeed, to be actually on their way towards the assumption of a snake-like form and habit, and it has been suggested that certain differences in the degree of development of the limbs upon which specific distinctions have been founded, are really due to individual variation, the species being in this respect in a state of unstable equilibrium. Be this as it may, in the common sand-skink (*Chalcides ocellatus*) the five toes are fully developed ; in *C. mionecton* they are reduced to four ; while in *C. lineatus* and *C. tridactylus* only three digits remain, while the fore-limbs are only about a quarter of an inch long in specimens measuring ten inches in length, although the hind pair is somewhat more developed. *Lygosoma lineo-punctatum* may be taken as an example of a species in which the digits are represented by a pair of toes, looking much like the pincers of a lobster. Finally, in *Chalcides guentheri* of Palestine, which is very similar to *C. tridactylus* but has the length of the body increased to fourteen inches, the limbs are reduced to stumps, without trace of their component digits. One step further on the same line of evolution, and we should have a snake-like skink.

As a matter of fact, such a type is represented by the members of the so-called family *Anelytropidae*, such as *Anelytropsis papillosus* of Mexico, and *Typhlosaurus* and *Feylinia* in

South and West Africa, which are really nothing more than worm-like limbless skinks, "degraded" for a burrowing life. Another somewhat similar type is represented by *Dibamus novæ-guineæ*, a worm-like burrowing reptile, with the hind-legs represented by a pair of small flaps, the limbs and even their supporting bony girdles being otherwise totally lacking.

Finally, we have a few small worm-like or snake-like lizards from California, constituting the genus *Aniella* and the family *Aniellidæ*, which seem to be degraded types more or less closely allied to the *Anguidæ*. Although soft overlapping scales are retained, the eyes and ears are concealed, and the limbs wanting. In the preceding and some earlier paragraphs allusion has been made to the degeneration of the eye in burrowing snakes, and certain modifications of the eyelids in some desert lizards. These may be briefly referred to collectively. In the burrowing snakes of the genus *Typhlops* the eyes are hidden by shields of the skin; but in the *Uropeltidæ* although small, they are distinct. In the burrowing lizards of the family *Aniellidæ*, the eyes, although concealed, are still present; and in the slow-worm, despite its misnomer of blind-worm, they are bright and bead-like. Accordingly, although the eye has been independently degenerated in several distinct groups of reptiles, in none has it become completely aborted, and in all cases probably retains some degree of functional power.

Very interesting is the independent development of a transparent "window" in the lower eyelid of two distinct groups of desert-haunting lizards, to which allusion has already been made. In the skinks of the genus *Mabuia* the lower eyelid has become much enlarged, so that it will cover the whole eye, its transparent window thus permitting of vision while the eye itself is protected from the sand-blast. In another group of skinks, forming the widely distributed Old World genus *Ablepharus*, the lower eyelid, which is completely fused to the margin of the aborted upper one, is wholly transparent; and these lizards consequently cannot "open their eyes" at all. Analogous modifications occur in desert lizards of the family *Lacertidæ*. This occurs, for example, in certain species of the Asiatic and African genus *Eremias*; in the Indian *Cabrita* the "window" is unusually large; and *Ophiops*, which is found in desert tracts in North Africa Syria and India, presents an exact

parallel to *Ablepharus*, the large and transparent lower eyelid being welded with its reduced fellow.

Adaptive modifications for protecting the ear and the nostrils from the intrusion of water or sand have been independently developed in many reptiles, for instance, desert-dwelling lizards on the one hand, and crocodiles on the other. In some cases the apertures of these organs are capable of being more or less completely closed by means of valves or fringes, while in other instances they are reduced to the size of mere pin-holes.

A large number of reptiles, living and extinct, have developed a bony armour in the skin, varying considerably in the different groups, and in many cases at any rate independently evolved. Very generally this bony armour, which is situated in the deep layer of the skin, is overlain by horny shields, which may or may not correspond with the bony plates beneath. In some of the extinct dinosaurs, such as *Scelidosaurus* and *Stegosaurus*, the dermal armour along the back is developed into bony plates and spines, probably sheathed during life in horn. At first sight the spines which fringe the back of many of the iguanas of the present day might well appear to correspond in structure (as they undoubtedly do in function) with the dorsal spines of these dinosaurs. As a matter of fact this is not the case, the spines of all the iguanas being nothing more than specially developed horny scales, and therefore of epidermal origin; none of the members of the family *Iguanidae* developing bony plates in the skin. Of the same horny nature are the spines on the body, limbs, and tail of the horned toads (*Phrynosoma*), which likewise belong to the same family. These reptiles have, however, true bony spines on the back of the head and along the sides of the lower jaw; these being attached to the skull itself, and therefore structurally comparable to the head-spines of the horned dinosaurs. The *Agamidæ* form another family of lizards characterised by the absence of dermal bony structures; accordingly the spines which cover the entire head, body, limbs, and tail of the oft-mentioned moloch lizard (*Moloch horridus*) are entirely epidermal horny structures. The same is the case with the spines girdling the tails of the agamoid lizards, of the genus *Uromastix*, and several other instances of the same nature might be cited. Never-

theless, all these spiny developments appear to be for the same purpose—namely, defence—as the bony spines of the dinosaurs, and therefore afford an example of how the same object is attained by different ends. Some of the leading types of bony armature in different orders of reptiles may now be passed in review, commencing with that of lizards.

The members of several families of lizards have bony plates in the skin beneath the scales, among these being the small Mexican group of *Xenosauridæ*, the girdle-tailed lizards (*Zonuridæ*), the blind-worms and their allies (*Anguidæ*), the poisonous lizards (*Helodermatidæ*), the African *Gerrhosauridæ*, and the skinks (*Scincidæ*). No more beautiful example of this armour exists than that of the glass-snake, or scheltopusik (*Ophisaurus apus*), a member of the *Anguidæ*, in which it forms a solid, although flexible, mosaic-like sheath investing the long snake-like body, and constituting, when cleaned, an exquisite structure. In the possession of this panoply the scheltopusik presents a contrast to the true snakes, in all of which it is lacking. In the girdle-tailed lizards the members of the typical *Zonurus* are covered with a coating of imbricating horny scales terminating in sharp spines which are largest on the neck, occiput, and tail in *Z. giganteus*. These are underlain by bony plates forming the basis of the spines, so that the armour is comparable to that of the dinosaurs.

In the New Zealand tuatera (*Sphenodon punctatus*), the living representative of the order Rhynchocephalia, the middle line of the hind portion of the head, back, and tail is surmounted with a row of partially erectile spines apparently similar to those of the iguanas. The tuatera's spines are said, however, to be of dermal origin and are covered with a thin sheath of horn, so that they seem structurally similar to those of the mail-clad dinosaurs.

All existing crocodiles and the great majority of their extinct relatives possess an effective dermal armour, consisting of movably articulated plates of bone overlain by horny shields. Most of these plates, as well as the upper surface of the bones of the skull have a pitted, or almost honey-combed structure, as is frequently the case when the greater part of the true skin is ossified. In modern crocodiles the plates of the dorsal buckler are arranged in more than two longitudinal

rows; while the transverse rows severally correspond with one segment of the skeleton of the trunk. In most species there is a detached patch of plates on the neck; and the larger scales on the back, like those of the neck-patch, are longitudinally keeled. As the tail is approached, the middle series of plates is gradually squeezed out, while the lateral ones approximate, till they finally meet in the middle line, where they lose their bony plates, with a proportionately greater development of the horny covering. In gharials (*Garialis* and *Tomistoma*), true crocodiles (*Crocodilus*), and true alligators (*Alligator*) the dermal armour is restricted to the upper surface, but in the African crocodile representing the genus *Osteolæmus* a few bony plates are developed in the throat, and in the caimans, or South American alligators (*Caiman*), a buckler of thin bony plates is developed on the abdominal surface. This ventral buckler comprises more than eight longitudinal rows of plates, each plate composed of two separate pieces of bone, connected with one another by suture. The degree of development of this armour varies in the different species, the culmination occurring in the high-crowned caiman (*Caiman palpebrosus*). In that species not only does the ventral armour cover the greater part of the lower aspect, but the limbs are invested in complete bony sheaths, which cover even the toes like gloves. The patch of plates on the nape of the neck is also connected with the armour of the back. Such a complete bony panoply appears to be met with elsewhere among living reptiles only in *Testudo emys* and a nearly related species. Why this particular species of caiman should require such a complex armour has not yet been ascertained.

In the crocodiles of the Jurassic epoch the armour differs considerably from that of existing types. In the family *Goniopholididæ*, for example, the dorsal plates are rectangular and may be arranged in two or in several longitudinal rows; while the ventral armour may form either a single or a double buckler, in which the posterior transverse rows of plates may overlap like the tiles on a roof, or may be articulated together by suture, each plate consisting of only a single element. In the typical *Goniopholis*, as represented by the "Swanage crocodile" of the Dorsetshire Purbeck, the plates of the dorsal buckler present the peculiarity of articulating with one another

by means of a peg-and-socket arrangement—a structure paralleled in some of the extinct armour-clad ganoid fishes. In the earlier family *Teleosauridæ*, on the other hand, the dorsal armour consists of two longitudinal rows of rounded plates; and the ventral buckler is divided into an anterior and a posterior portion, in which the component plates (each formed by a single piece) of the hind transverse rows are united by suture. The dorsal buckler of *Pelagosaurus* affords an admirable illustration of the type characteristic of the *Teleosauridæ*.

From the foregoing comparisons it will be apparent that while in the anterior region of the ventral buckler of all crocodiles in which this is developed the component plates of each transverse row articulate with one another by a sutural union, in the posterior moiety of this buckler in the Jurassic forms the articulation of the transverse rows may be either by suture, or by imbrication. Here, again, we are unable to account for these structural differences.

Finally, as mentioned elsewhere, in the marine Jurassic crocodiles of the genera *Geosaurus*, *Dacosaurus*, and *Metrorhynchus* the dermal armour, in adaptation to the needs of a pelagic existence, has been discarded.

In the belodonts of the Trias, comprising the genera *Phytosaurus*, *Stagonolepis*, and *Parasuchus*, which are referred by some authorities to the Crocodilia, while by others they are regarded as representing an order (Parasuchia) by themselves, there was also a pitted dermal armour very similar to that of the true crocodiles. In all the genera the dorsal plates are keeled and form two longitudinal rows with a few smaller lateral series; while those of the ventral armour, which is present in *Stagonolepis* but absent in *Phytosaurus*, are arranged in not more than eight longitudinal rows, with each plate consisting of only a single piece. Whether we regard the dermal armour of the belodonts and of the true crocodiles as inherited from a common ancestor, or independently developed in each case, must largely depend upon the view taken as to the affinity of the two groups.

Other crocodile-like reptiles from the Trias, such as *Aëtosaurus*, with pitted dermal armour, were apparently more or less intimately related to the belodonts; but it is at present impossible to say whether their armature has been derived from a

stock which gave rise to crocodiles, or to crocodiles and belodonts together, or whether it is an independent development. In a remarkable reptile from the Trias of America known as *Typhthorax* the pitted bony plates are said to be adherent to the ribs, and it has been suggested that this fore-shadowed the carapace of the Chelonia. The wide skeletal differences between tortoises and turtles on the one hand, and crocodile-like reptiles on the other, demonstrates, however, that such a feature cannot be regarded as indicative of the origin of the chelonian carapace, and that, if really existing, it must be a special development.

Despite the marked structural resemblances of the extinct dinosaurs to the primitive crocodile-like reptiles such as the belodonts, it is evident that the dermal armaments developed in many members of the former group have been evolved independently of those of the latter. The armour of some of these huge reptiles was of a most effective and often of a most bizarre type. Some of the later representatives of the group in which it occurs also developed large horn-like processes on the skull comparable to those of certain extinct Tertiary mammals such as the Dinocerata and Uintatheria; such a development of horn-like structures in the later members of a group being apparently a sign of over-specialisation and impending extinction.

The armoured dinosaurs, in contradistinction to the horned section, form a group (Stegosauria) nearly allied to the iguanodons. The earliest known representative seems to be *Scelidosaurus harrisoni* from the Lower Lias of Lyme-Regis, Dorsetshire. In this species, which was about the size of an average crocodile, although with a small head, there appear to have been two longitudinal rows of keeled bony plates running from the neck along the back, and converging into a single row on the upper surface of the tail; while the sides and flanks were defended by numerous rows of smaller plates. *Hylaeosaurus*, of the Sussex Wealden, seems to have been a nearly allied although much more imperfectly known type, in which the plates along the back were developed into long and laterally compressed spines; the precise mode of arrangement of these spines being still unknown, although it was probably very similar to that obtaining in *Polacanthus foxi* of the Wealden



FIG. 8.—Restoration of skeleton of an Armoured Dinosaur (*Polacanthus forzi*). After Baron.

*Notesa.*

of the Isle of Wight. The latter was a remarkable dinosaur, in which, in addition to a double row of broad compressed spines along the neck and back, a huge solid buckler, dotted over with prominent bosses to which other spines were articulated, protected the whole of the hind quarters. The lumbar shield, as in tortoises, is firmly welded to the pelvis.

The dermal armour is most completely preserved in the genus *Stegosaurus*, represented by species from the Upper Jurassic strata of North America, and having a near ally in the Kimeridge Clay of England, which has been described under the name of *Omosaurus*. In this ungainly monster, which measured close on thirty feet in length, with an extreme height of ten feet, the dermal armour took the form of two parallel rows of vertical crest-like plates gradually in-

creasing in size from the nape of the neck to the loins, where they are about a yard high and as much in basal length. Towards the tail they again begin to diminish in bulk, and on the terminal part of that appendage they are replaced by four or five pairs of long and stout spines, which may be compared to marline-spikes. Structurally these vertical plates appear to be an ultra development of the longitudinal low keels on the plates of crocodiles.

Stranger still is the armature of the horned dinosaurs of the Cretaceous of North America, as represented by *Triceratops flabellatus* and its allies, which mark the culminating point of dinosaurian development in the way of armature. *Triceratops* takes its title from the presence of three bony horn-cores on the skull, of which two form a pair above the eyes, while the third is situated on the nose, after the manner of the horn of the Indian rhinoceros. The most extraordinary feature in the skeleton of these reptiles is, however, the huge flange-like shield projecting backwards from the occipital region of the skull, and completely covering the anterior vertebræ of the neck. In life, it seems most probable that the bony horn-cores were ensheathed with horn, in which case this armature would be precisely comparable to the horns of oxen and antelopes among ruminant mammals. In some of these monsters the length of the skull, inclusive of the neck-shield, was little short of seven feet. Small dermal bony plates extended some distance behind the posterior margin of the neck-shield, but the body of *Triceratops* was not protected by armour. On the other hand, certain allied types, such as *Nodosaurus*, appear to have been furnished with a nearly complete panoply.

The most typical of all armoured reptiles are the members of the order Chelonia, that is to say the turtles and tortoises, in which a "shell" of bone is developed from dermal elements, and more or less completely encloses the body. To describe in detail the structure of this shell would be out of place, and it must suffice to say, firstly, that it consists of an upper half, or carapace, and a lower moiety, or plastron. In some cases, as in ordinary land-tortoises, the carapace is joined to the plastron by a bony bridge, so that the whole structure forms a solid box into which the head, limbs, and tail can be withdrawn; the horny beak and the horny shields on the limbs effectually guarding

the apertures in front and behind. In certain instances, as in the box-tortoises, more effectual protection is afforded by the development of transverse hinges in the plastron, which is thus provided with movable flaps, completely closing the two aper-

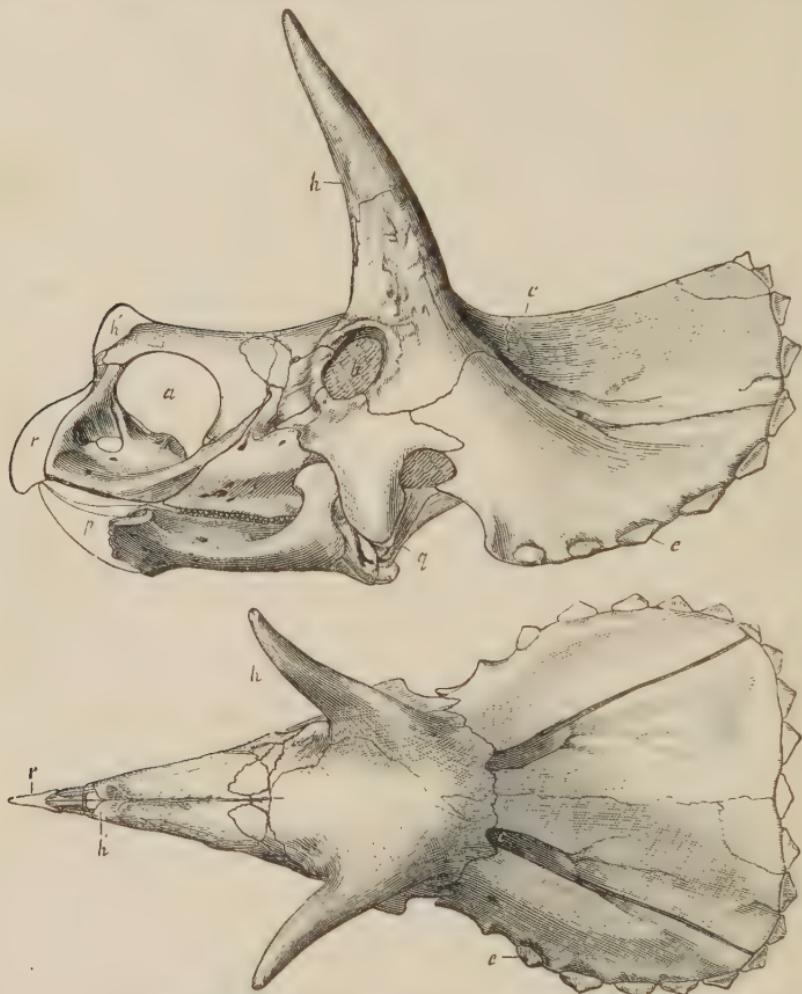


FIG. 9.—A, lateral, B, dorsal views of the skull of a Horned Dinosaur (*Triceratops flabellatus*) showing horn-cores and neck-shield. *a*, nostrils; *b*, orbit; *c*, supratemporal vacuity; *e*, small bones round occiput; *h*, left horn-core; *h'*, horn-core on nose; *p*, predentary bone; *q*, quadrate bone; *r*, rostral bone.

tures when the animal is withdrawn into its shell. On the other hand, in the marine turtles, which do not require such complete protection, the upper and lower halves of the shell are disconnected, and the head and neck cannot be drawn within the margins of the carapace. As mentioned in an earlier paragraph, the

chelonian skeleton is remarkable for the circumstance that the shoulder and pelvic girdles lie within—instead of without—the ribs. Consequently the upper plates of the carapace lie directly upon the spines of the vertebræ and the ribs, to which they ultimately become welded. The marginal plates of the carapace have, however, no subjacent stratum belonging to the internal skeleton. As regards the plastron, it will be sufficient to state that while its three anterior elements respectively represent the clavicles (collar-bones) and inter-clavicle of other vertebrates, its hind constituents appear to correspond with the so-called abdominal ribs found on the ventral aspect of the body in crocodiles, plesiosaurs, and tuateras. Evidently, then, chelonians are descended from a group of reptiles furnished with such a system of abdominal ribs, but beyond this we are in the dark as regards their ancestry.

As in crocodiles, the dermal bony armour of most tortoises and turtles is overlain by a series of horny shields; but there is the important difference that whereas in the members of the former group the epidermal horny shields correspond in size and in number with the subjacent dermal bony plates, in the latter group they do not so correspond. As a matter of fact, although there is a general agreement in the plan of both the horny shields and the bony plates, the former are fewer in number and larger in size than the latter, and cover portions of the series to which they do not pertain. It is consequently believed that the two structures have been developed independently of one another at different stages of the evolution of the group, the horny plates being presumably the older. That is to say, the ancestral chelonians are believed to have been protected by horny shields alone, and to have had no bony dermal armour. The final stage of evolution, so far as the covering of the body is concerned, is the loss of the horny shields, which in the soft river-tortoises of the family *Trionychidæ* are replaced by a continuous leathery skin.

Such are the general features of the chelonian shell. In the luth, or leathery turtle (*Dermochelys coriacea*), now representing the family *Dermochelyidæ*, the shell is of a different type. It is described by Dr. H. Gadow in the volume on reptiles in the *Cambridge Natural History* in the following words:—

“The dorsal and ventral halves are directly continuous,

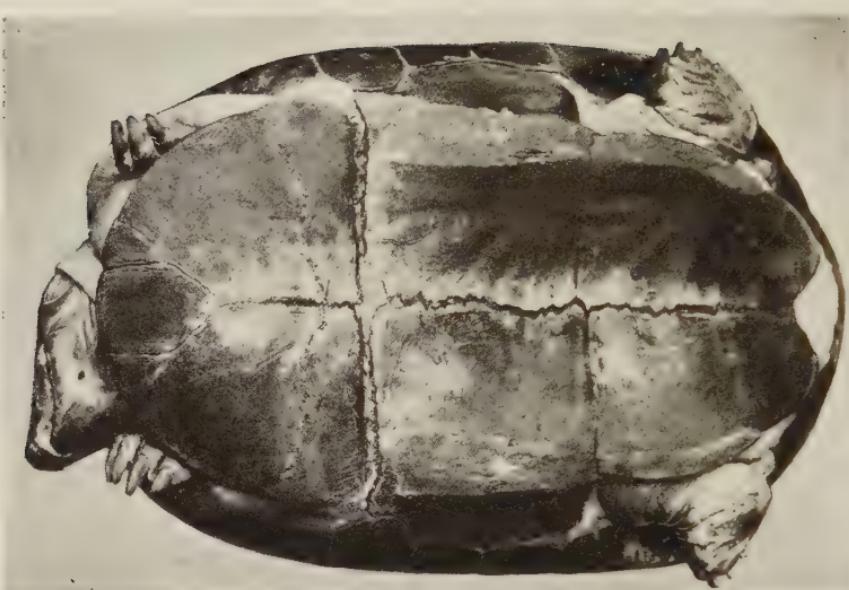
forming one unbroken case all round, which is composed of many hundreds of little bony plates, irregularly polygonal, fitting closely into each other with their sutural edges, and giving the shell a beautiful mosaic appearance. On the dorsal side are a median row and three pairs of lateral rows of larger plates, and these form seven longitudinal blunt ridges which all converge towards the triangularly pointed tail-end of the shell. . . . The mosaic plates are deeply embedded in the cutis [skin], being externally as well as internally covered or lined with dense leathery skin. The epiderm is thin and shows no indication of horny scales. In young specimens the whole shell is soft and very imperfectly ossified, later on it is quite rigid, although comparatively thin. It is nowhere in contact with the internal skeleton, except by a nuchal [nape] bone, which by a descending process articulates with the neural arch of the eighth cervical [neck] vertebra."

As already mentioned, different views are entertained with regard to the relationship between the shell of the luth and that of typical Chelonia. According to one view, the luth's shell is a degenerate modification from that of the true marine turtles; according to a second the two have nothing in common, and leathery turtles form a group distinct from all other Chelonia. An attempt to reconcile such opposite opinions has been made by regarding *Dermochelys* as the most specialised of all Chelonia, but at the same time derived from terrestrial forms independently of the *Chelonidæ*. Another view is that the mosaic plates of the luth correspond to the bony plates of crocodiles, while the plates of the shell of other chelonians are of different type, and correspond (as those of the plastron certainly do) to the category of abdominal ribs. If this be true, the *Chelonidæ* and the *Dermochelyidæ* indicate independent types of diverse origin. The same must be the case if certain mosaic-like dermal plates from the German Trias described as *Psephoderma* really belong to an ancestral form of leathery turtle.

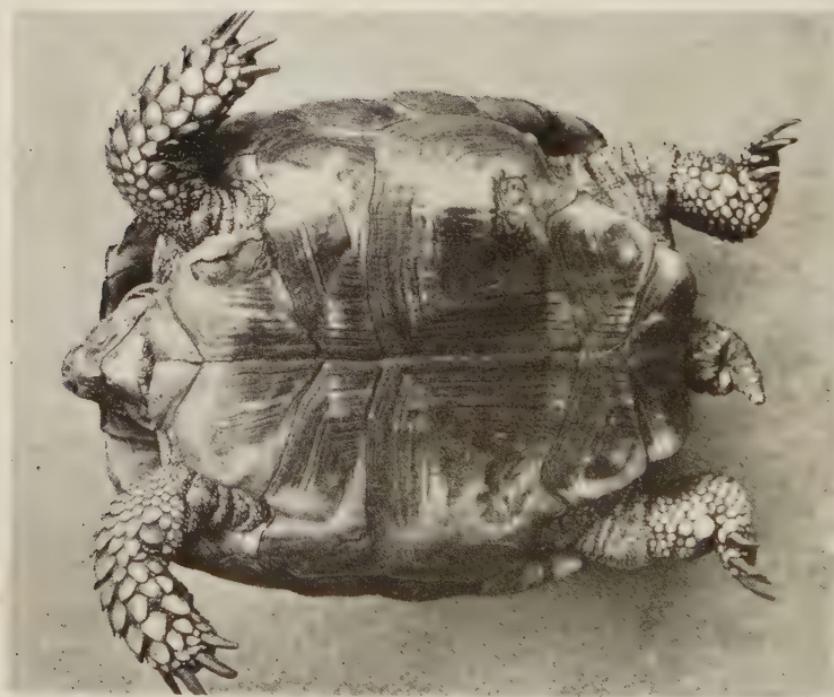
This notice of defensive adaptation in chelonians may be closed by a second quotation from Dr. Gadow's work, dealing with general structural adaptations in the group:—

"Nearly the whole organism," he writes, "has been altered. The hard, firm carapace has partly rendered the supporting





SIDE-NECKED (PELOMEDUSAVARIABILIS) TORTOISE,  
*LAURENTI'S ARCO,*  
TO SHOW HOW THE HEAD IS WITHDRAWN BY A  
VERTICAL S-LIKE CURVE



SIDE-NECKED (PELOMEDUSAVARIABILIS) TORTOISE  
(STEREOCENTROCHELYS NIGER) TO SHOW HOW  
THE HEAD IS WITHDRAWN BY A LATERAL  
FLEXURE OF THE NECK

functions of the vertebral column unnecessary or impossible. In many tortoises, especially in the large land-tortoises, the vertebræ and the capitular portions [heads] of the ribs are reduced to mere bony outlines; the reduction to these paper-like bony lamellæ proceeds with age. The iliac [upper pelvic] bones find a better support in the costal plates; the contact with the sacral ribs is given up, and these ribs fuse partly with the costal plates, or they are absorbed. The whole mass of muscles of the trunk is completely lost in the region of the shell, but traces of them exist in young specimens. Neck, limbs, and tail can in most cases be withdrawn and hidden in the shell. When this is not possible, it is due to secondary changes. The neck is withdrawn either by being tucked away sideways (Pleurodira), or by being bent in an S-shaped curve in a vertical plane (Cryptodira). In a left-sided profile view of the animal, the head represents the tail of the S. The neck is withdrawn by long muscles, which are inserted into the ventral side of the middle of the neck, and extend in the shape of vertical ribbons far back into the shell, arising from the centra [bodies] of some of the middle or even more posterior thoracic [trunk] vertebræ."

It should be added that certain giant land-tortoises inhabiting the Galapagos Islands (where there are no large animals to attack them) have undergone a kind of retrograde development in the matter of dermal armour, the bony plates of the carapace having become so thin that they can be pierced with a penknife. This is an instance of the tendency in nature to dispense with an organ or structure when it is no longer of use.

A few of the Triassic anomodont reptiles, such as *Elginia* and *Geikia* have developed horn-like processes on the skull comparable to those of the horned dinosaurs, and perhaps also sheathed in horn during life. Whether these reptiles had a dermal armour does not seem to have been ascertained.

## CHAPTER VIII

### ADAPTATIONS (CONTINUED)—ADAPTATIONS TO SPECIAL ENDS

Devices for diminishing weight. Shoulder-girdle and pelvic girdle of tortoise tribe. Devices in regard to movement and breathing under water. Beaks and teeth in relation to food. Poison-fangs. The chamæleon's tongue. Blood-squirting from the eyes. Skin-secretions. Spitting. Fluid exudations. Hissing and intimidation. Death-feigning. Immunity to snake-venom. Lungs of chamæleons and snakes. Voluntary fractures. Rattlesnake's rattle.

**I**N the first portion of the preceding chapter attention has been directed to the amount of adaptive variation occurring in the external form of reptiles. Naturally such differences must be correlated with not less important differences in the skeleton, and it is some of the more striking of these that now claim attention. During the latter part of the Mesozoic epoch, that is to say, the Upper Jurassic and Cretaceous periods, there existed reptiles which have never been rivalled in the matter of corporeal bulk by any other land animals. Some of the largest of these dinosaurs such as *Diplodocus* and *Brontosaurus* (or *Apatosaurus*) measured about sixty feet in length, and stood something like twenty feet high at the loins, which was the most elevated part of the body. In the case of such monsters it is manifest that if the whole skeleton were solid its weight would be such that either the creature would be unable to move or that the bones would crush one another by their mere dead weight. Obviously the only practicable course was to lighten the skeleton. To effect this by making the limb-bones hollow would, however, have been out of the question, as bone has not the strength of iron, and hollow columns of the former would have been crushed under the weight of the enormous carcase. On the other hand, it would be feasible to lighten the skeleton by making the vertebral column hollow; and this has been actually done, the bodies of the vertebrae of these monsters having large cavities on the sides communicating with hollows in the interior.

Lightness is also produced by the adoption of the T-iron principle in the construction of the trunk-vertebræ of these reptiles, which show a number of buttress-like supports of this nature. In consequence of this arrangement the vertebræ of these gigantic herbivorous dinosaurs did not weigh much more than half as much as those of whales of equal bulk ; and it is probable that the entire weight of the largest species was not more than some forty or fifty tons instead of sixty or seventy.

Honey-combed and buttressed vertebræ of this type are found only in the so-called sauropod dinosaurs, which walked on all fours, and were probably to a great extent aquatic. Indeed, if their habits were not aquatic, it is doubtful if these reptiles could have attained such huge size. The need of lightness in the skeleton appears, however, to have been equally felt in the carnivorous, or theropod, group, most, if not all, the members of which habitually walked in the upright posture. In the case of species like the large megalosaurs, which probably stood fifteen or twenty feet high, lightness of skeleton was essential on account of the great bodily size ; but in certain much smaller forms, such as *Cœlurus* and *Calamospondylus*, it appears to have been required in order to admit of great bodily activity and speed, some of these small dinosaurs, as already stated, having perhaps been in the habit of catching and killing the contemporary long-tailed birds. Be this as it may, in *Megalosaurus* and its relatives both the limb-bones and the bodies of the vertebræ were hollow internally (and probably filled with marrow during life) ; while in *Cœlurus* and *Calamospondylus* the entire vertebræ consisted of little more than a thin shell, the whole interior being hollow. As the vertebræ of these theropods differ markedly in structure and the manner in which they are hollowed out from those of the sauropods, it is clear that the lightening process has taken place independently in the two groups. This, however, is by no means all, for the iguanodonts, or bipedal herbivorous dinosaurs, in which the vertebræ are solid, also have hollow limb-bones, and these would appear to have acquired this structure independently of the carnivorous group.

One other group of reptiles, namely the pterodactyles (Ornithosauria), to which lightness of body was a matter of vital importance, achieved it in the same manner as birds ; their bones

being mere hollow shells, with the cavities filled with air derived from the windpipe. A small perforation in each of these pneumatic bones marks the point of entry of the air-tube. The occurrence of this pneumatic condition in the bones of both birds and pterodactyles is perhaps the most remarkable instance of the independent development of an important structural adaptive feature to be met with in nature, implying as it does the correlated modification of several totally distinct parts of the organism. It may be added that the breast-bone, or sternum, of pterodactyles is furnished in the middle line with a prominent vertical ridge, or keel, for the attachment of the powerful muscles essential to flight, thereby presenting another adaptive resemblance to birds.

All tortoises and turtles, with the exception of the leathery turtle and its extinct relatives, present the peculiarity that the dermal armour is welded with the ribs so as to form one solid whole. This being the case, it will be obvious that the shoulder and pelvic girdles cannot occupy their normal position between the ribs and the skin (that is to say the dermal armour). The difficulty, as already mentioned, has been got over by transferring the bones of the shoulder-girdle and the pelvis to a position inside the ribs.

Many profound modifications of the skeleton have been brought into existence in connection with the various modes of motion characteristic of different groups of reptiles.

The most striking and conspicuous of these occur in the limbs of the marine forms, among which it is interesting to notice how the same end has been attained by different means. One remarkable modification in the structure of the vertebræ seems to be connected with motion. In most groups of reptiles, as in the higher vertebrates generally, the vertebræ are movably connected with one another by means of two pairs of flattened articular facets or surfaces, technically known as prezygapophyses and postzygapophyses. Such a mode of articulation serves perfectly well for creatures with bodies of moderate length and flexibility; but it is conceivable that it would be insecure and liable to dislocation in reptiles with the elongated and flexible bodies of snakes. It is, therefore, not surprising to find that in those reptiles the vertebræ are provided with two additional pairs of articulations, namely the projecting zygo-

sphenes and the cavernous zygantra, the former of which fit into the latter after the fashion of a tenon-and-mortice joint. Neither is it a matter for wonder to find similar articular surfaces developed in the vertebræ of the extinct sea-serpents, or Pythomorphæ, as well as in some of the members of the group Dolichosauria, which is likewise extinct. What does give rise

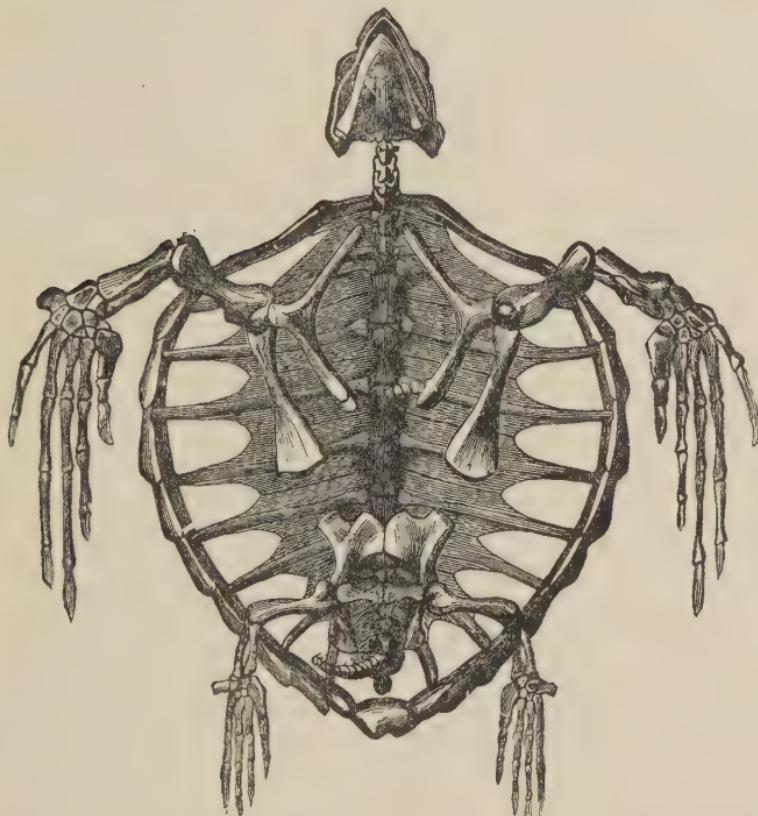


FIG. 10.—Ventral view of the skeleton of the existing Logger-head Turtle (*Thalassochelys*) with the plastron removed, to show the position of the shoulder-girdle and pelvis within the ribs. From *Guide to Fossil Reptiles, Amphibians, and Fishes in British Museum (Natural History)*.

to wonderment, is, however, the fact that while these zygosphenes are absent in the *Anguidæ* (slow-worm and glass-snake), except in a rudimentary condition in one genus, they are fully developed in the iguanas. If snakes require them, why are they also not essential to glass-snakes and blind-worms, and if monitors and other lizards can dispense with them, why are they developed in iguanas? Possibly the answer to the first part of the question is that the *Anguidæ* do not climb, and that additional articu-

lations are only essential to climbing snake-like reptiles. To the second part of the question no answer seems forthcoming. This, however, is not all, for we must either regard iguanas as the direct ancestors of snakes, sea-serpents, and dolichosaurians, or we must consider that zygosphenes were present in the ancestral stock of all the Squamata, or, finally, that they must have been developed independently in each of the groups in which they occur. If the latter be the solution of the puzzle, it is marvellous that these structures should be practically identical in all the groups.

Passing on to modifications in the skeleton of the limbs, we have to notice the fore-limbs, or "wings," of pterodactyles. In these there is nothing remarkable, so far as length is concerned, in either the first (humerus) or second (radius and ulna) segments; the metacarpus is, however, so lengthened as to be equal in this respect to the radius and ulna, but the real carrier of the wing is the enormously elongated fifth or outer digit (the first being lacking), each of the first three joints of which is considerably longer than the radius. In the mode of construction of the wing, pterodactyles therefore present no sort of parallelism to birds. It may be added that in some of the earlier forms (*Dimorphodon*) the proportionate length of the metacarpus is much less than that mentioned above.

The second noteworthy modification of the fore-limb occurs in the iguanodon, in which the first digit, or thumb, has assumed the form of a short and thick conical spine, which was probably sheathed with horn during life and may have been employed in fighting.

Turning to marine forms, in which the limbs were modified into flippers or paddles, we find the simplest skeletal type of this kind in the turtles, in which the bones of the digits are abnormally lengthened, without any increase in number, or marked alteration in their form. Moreover, the bones of the upper segments of the limb (humerus and radius and ulna) are not abnormally shortened. Much the same may be said with regard to the extinct pelagic crocodiles. When, however, we come to the extinct sea-serpents, or Pythonomorpha, we find that while the digits are so normal, the aforesaid three bones of the upper segments have become shortened and widened, that their lengths scarcely exceed that of the first row of bones in the digits.

A more advanced and specialised type of skeleton is presented by the paddles of the plesiosaurs. Here the fore and hind paddles are nearly of a size and the humerus (or upper bone) in the one and the femur in the other, although much expanded inferiorly, retain the characters of "long bones". The radius and ulna in the fore-paddle and the tibia and fibula in the hind pair have, however, altogether lost this character, being much shortened and laterally expanded, so that they are practically similar to the bones of the carpus and tarsus which respectively come below them. Furthermore, although the bones of the metacarpus (in the fore-limb) and metatarsus (in the hind-paddles) and of the digits (in both) retain much the normal contour and proportions, yet the number of phalangeal bones in each digit is increased beyond the ordinary. If, however, we trace the plesiosaurs down into strata of Triassic age we find all the bones of a more normal type, this being especially noticeable in the case of the radius and ulna and the corresponding elements in the hind limb. These early sauropterygians were, indeed, at most only partially aquatic, and certainly not marine.

Of a totally different and more specialised type is the limb-skeleton of the ichthyosaurs (*Ichthyopterygia*), in which the front-paddles were approximately double the size of the hind pair. In the Liassic members of this group with the most complicated type of paddle the humerus, although retaining in a modified degree the character of a "long-bone" has become greatly shortened and thickened; but the whole of the bones below this have come to resemble those of the carpus in general character, so that they form a continuous mosaic-like pavement, with no separation of the digits. Not only has the number of individual bones in each digit been largely augmented, but the number of digits has been increased above the normal five, apparently by the splitting, or forking, of some of them. In none of the bones of the digits is there any trace of a division into a "shaft," and two terminal "heads" or expansions; that is to say, they have entirely lost all traces of evidence that they correspond to "long bones," like those in the paddles of the turtles or in the feet of terrestrial reptiles.

If, however, we trace the ichthyosaurs down into the Trias, we find that their paddles show distinct evidence of derivation

from reptiles with limbs of more normal structure. For instance, in the genus *Merriamia* the humerus is longer and more constricted in the middle than is the case in *Ichthyosaurus*; while the radius and ulna (as also the tibia and fibula in the hind-limb) likewise retain the characters of "long bones," their length markedly exceeding their width, while they are constricted in the middle and separated from one another by a space, so that they are essentially different in character from the bones of the carpus by which they are succeeded inferiorly. Again, the carpus bones themselves as well as those of the digits are proportionately longer and less squeezed together than in *Ichthyosaurus*. It will also be noticed that the external margins of the bones of both the outer and inner digits (such digits being only three in number) are notched. That such notches represent the last vestiges of the shafts of "long bones" can scarcely be doubted, despite the fact that they also occur in the bones of the carpus (the two transverse rows immediately below the radius and ulna) which are not normally "long bones".

Beyond this stage it has not been found possible to carry the derivation of the complex paddle of the Liassic ichthyosaurs, but it may be taken for granted that if we had the full series of forms, we should find a transition to reptiles with limbs adapted for terrestrial movement. It may be added that in the supreme culmination of the ichthyosaurian stock (*Ophthalmosaurus*) three bones articulated with the humerus in place of the two characteristic of *Ichthyosaurus*.

Finally, it is scarcely necessary to emphasise the fact that all the various types of paddles referred to in the preceding paragraphs have been evolved independently of one another from terrestrial or semi-aquatic reptiles.

In the majority of reptiles the nostrils open posteriorly into the mouth near the front or middle of the palate, so that the tube connecting the external, or true nostrils, with the internal or posterior nostrils (*choanae*) is comparatively short. In modern crocodiles and gharials, on the other hand, the posterior nasal apertures have been carried back close to the occipital region of the skull; this adaptive arrangement being brought about by the development of a secondary flooring to the skull, or what would be called in human anatomy a back-

ward prolongation of the hard palate. In most reptiles only the premaxillæ develop palatal plates to form this secondary flooring, but in modern crocodiles such plates are also developed by the maxillary, palatine, and pterygoid bones, in consequence of which the choanæ open immediately in front of the occipital condyle. As the result of this arrangement the posterior apertures of the nasal passages are brought (by means of an elongation of the latter) into direct communication with the wind-pipe, or trachea, and crocodiles are thus enabled to open their mouths and hold their prey under water and yet, by keeping their nostrils above the surface, to breathe all the time without difficulty. A similar structural adaptation occurs in whales and dolphins; but is wanting in the completely marine ichthyosaurs and plesiosaurs, and it is consequently difficult to understand how those reptiles managed to hold and swallow their prey in the water, unless indeed the nasal passage was prolonged backwards by means of some special arrangement of the soft parts. The same remark applies to the Mesozoic pelagic crocodiles (*Geosaurus*, etc.) and the sea-serpents (*Pythonomorpha*); but the ordinary Mesozoic crocodiles, such as *Teleosaurus* and *Steneosaurus*, in which the apertures of the posterior nostrils were situated far forward on the palate, may have carried their prey to land. An extinct crocodile (*Leidyosuchus*) from the Cretaceous of North America presents an intermediate condition; the choanæ opening in the middle of the pterygoid bones.

Another group of reptiles in which the posterior apertures of the internal nostrils are carried far back (although not to the same degree as in modern crocodiles) by the development of a secondary floor to the palate is the genus *Lytoloma*, which includes marine turtles of Lower Eocene and Upper Cretaceous age. In this case, which has been evolved independently of the crocodiles, it has been suggested that the arrangement is connected with the great backward extension of the bony union, or symphysis, of the two branches of the lower jaw: and it has been thought that the latter feature indicates that the food of these turtles consisted of shell-bearing molluscs.

Be this as it may, it is clear that the extinct turtles of the genus *Lytoloma* resembled their modern marine cousins and the other members of the order Chelonia generally in that the

jaws formed a horny beak devoid of teeth. This gives an opportunity to direct attention to the fact that several groups of reptiles have developed independently of one another horn-sheathed beaks and discarded teeth. That such a development is in some manner connected with food and feeding, may be considered almost certain; but it is difficult to say what is the precise reason for the modification, seeing that while forms with beaks, such as a large number of chelonians, are herbivorous, the pterodactyles were carnivorous. The Chelonia are the only ordinal group of reptiles of which all the members have discarded teeth in favour of a horny beak; and we are still in the dark as to the kind of toothed reptiles from which tortoises and turtles are descended. There are, however, several groups of which the later and more specialised representatives have lost all or most of their teeth and acquired a cutting beak, probably ensheathed during life in horn. Among such reptiles are the dicynodonts, belonging to the order Anomodontia, in which the males at any rate retained a pair of large tusks in the upper jaw, but had the rest of the jaws converted into a cutting beak. In certain other skulls, which probably indicate the females of *Dicynodon*, although they have been referred to a genus apart (*Udenodon*), even the single pair of tusks was lacking and the entire jaws were beak-like. The pterodactyles present another instance where the more specialised types (*Pteranodon*, etc.) have replaced teeth by a horny beak; and the same seems to have been the case with the specialised ichthyosaurs of the genus *Ophthalmosaurus*, in which, however, a few small functionless teeth may have persisted.

Reverting to the giant pterodactyles, it may be mentioned that in point of size a species from the Cretaceous strata of Kansas exceeded the largest albatross, the span of wing being no less than 23 ft., while the skull is little short of 40 in. in length. The latter dimension is, however, calculated to give an exaggerated idea of the size of this "dragon," for the skull is extended nearly as far behind the vertebral column as it is in front. In fact, this part of the skeleton resembles a crutch-stick or a pickaxe, the vertebral column forming the stick and the skull the cross-bar. Apparently this backward extension of the occipital region of the skull was intended as a counter-

poise to the beak, although if large-billed birds like the adjutant stork can manage to get on without such a structure it is difficult to imagine why it should be necessary in the case of the pterodactyle. Another feature of this giant pterodactyle is the presence in the socket of the eye of a ring of bones, comparable to those found within the eyes of birds. The existence of this "sclerotic ring" of bones in the eye of the larger pterodactyles is an instance of a parallel adaptive character, for it is unknown in the smaller members of the group, and since pterodactyles have no relationship with birds, it must have been acquired independently in the two groups. Another instance of the same kind is the loss of the teeth in both these groups; the more primitive birds, like the oldest pterodactyles, having the jaws armed with a full series of sharply pointed teeth. Pterodactyles of all kinds doubtless fed, like gulls and cormorants, on fish, and at first sight it might seem that toothed jaws were better adapted to hold such slippery prey than is a smooth horny beak. It has, however, to be borne in mind that although such toothed jaws would ensure the retention of every fish captured, yet they would prove a hindrance to its being swallowed quickly and easily. Possibly it would have been necessary for a toothed bird or a toothed pterodactyle to resort to the shore before being able to devour its prey; and if this be the case we should have an explanation of the reason why both birds and pterodactyles discarded teeth in favour of a horny beak, which enabled them to bolt their food while on the wing.

The dinosaurs of the iguanodon group have undergone a still more remarkable development in connection with the formation of a beak, for in these herbivorous reptiles an additional and separate toothless bone—the predentary—was developed at the tip of the lower jaw, and formed with the equally toothless premaxillæ, or anterior paired bones of the upper jaw, the muzzle. Whether in this instance the beak was sheathed in horn may be doubtful.

A further stage is presented by the horned dinosaurs, such as *Triceratops*, of the Upper Cretaceous strata of North America, in which a separate bone (the prerostral) was developed at the tip of the upper jaw, so as to correspond with the predentary below; and it is generally believed that in these reptiles a horny sheath cased the entire beak.

From horny beaks, with or without a pair of tusks in the upper jaw, the transition is easy to teeth, since both, in a greater

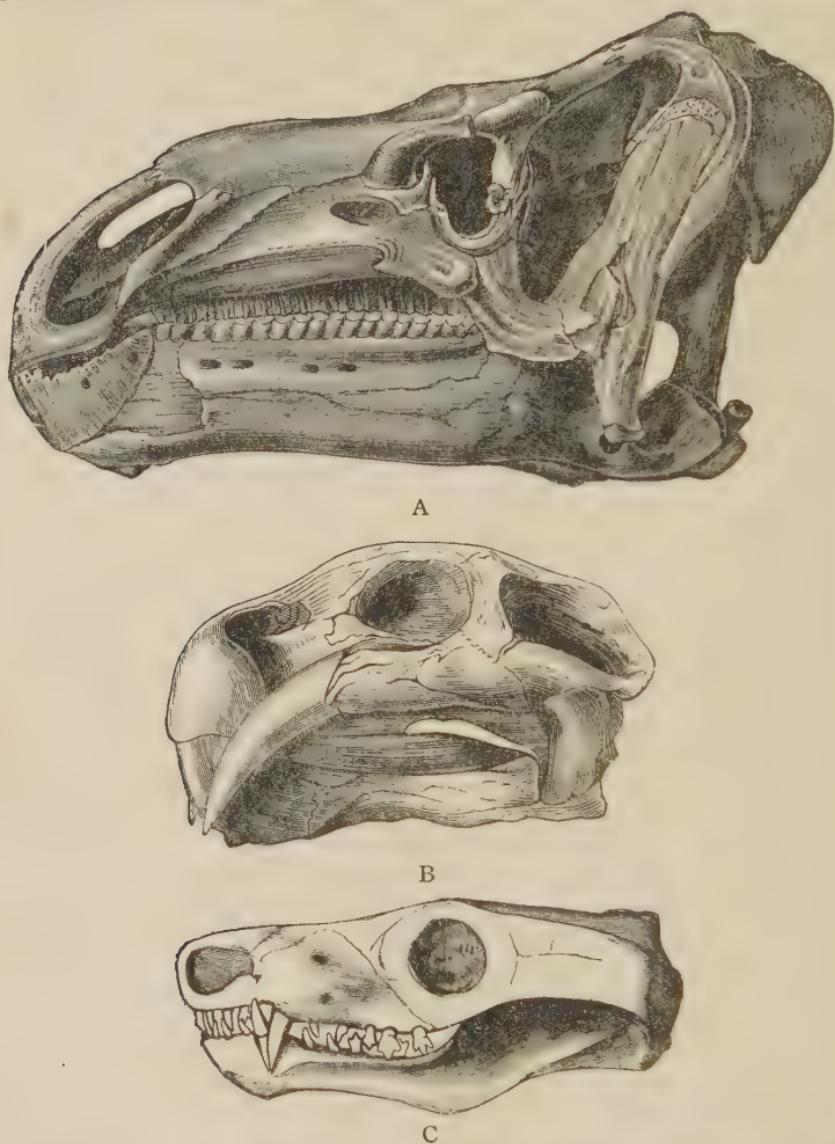


Fig. 11.—A, skull of Iguanodon, to show predentary bone and edentulous fore part of jaw. B, skull of Dicynodon, showing single pair of upper tusks, and horny beak. C, skull of Carnivorous Mammal-like Reptile (*Galesaurus*) to show differentiated dentition. A and B from *Guide to Fossil Reptiles, etc., in British Museum (Natural History)*.

or lesser degree, are connected with the nature of the food, and are therefore to some extent, at any rate, adaptive in this respect. Furthermore, the teeth may also be intimately connected

with attack or defence, and may thus be adaptive in another

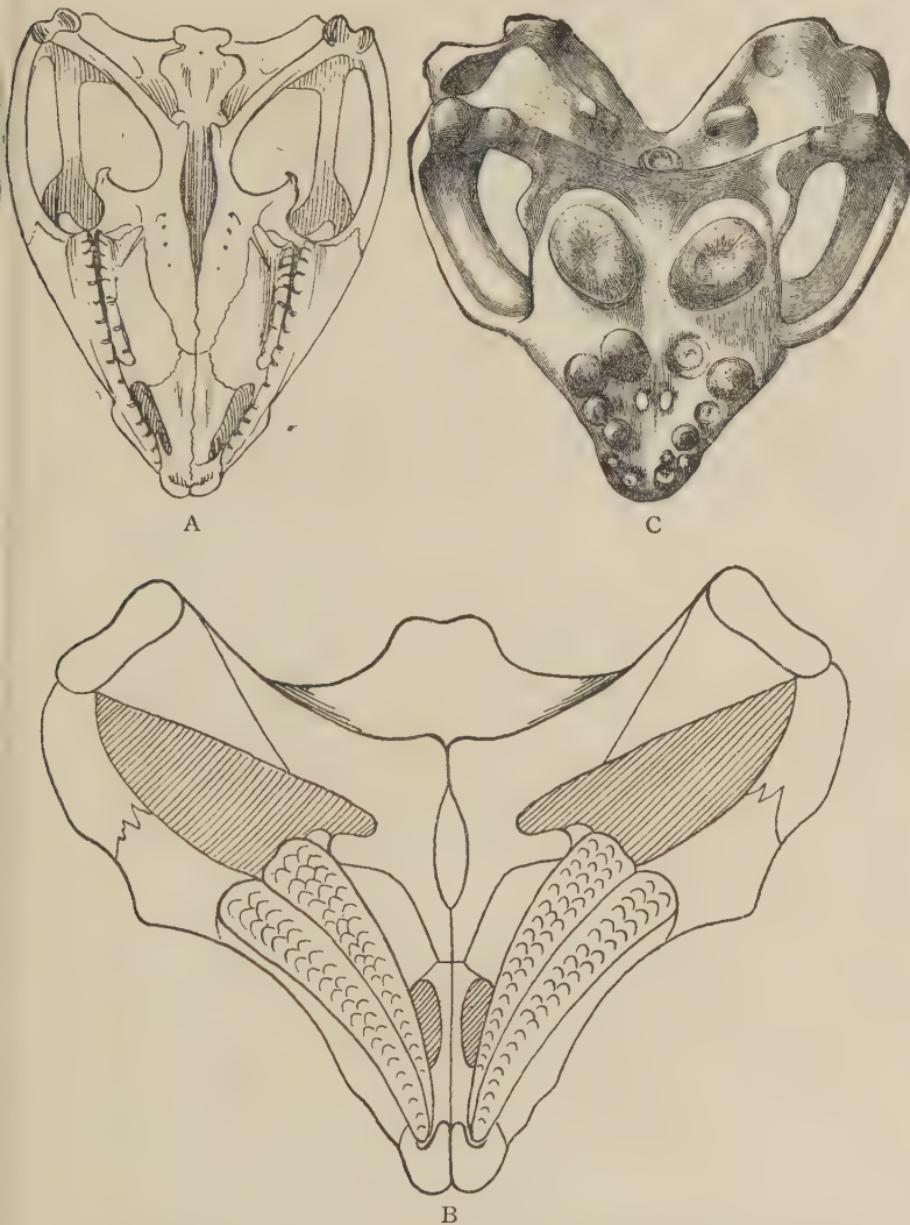


FIG. 12.—Palatal view of dentition of existing Tuatera (A), and extinct Pavement-toothed Tuatera (B). C, Palatal view of dentition of Bean-toothed Reptile (*Cyamodus*). B, after Boulenger. C, from *Guide to Fossil Reptiles, etc., in British Museum (Natural History)*.

sense; thereby forming a connection between adaptations in relation to food and adaptations for attack and defence. The

numerous types of dentition occurring in reptiles will be noticed but briefly; attention being directed only to some of the more remarkable types.

Before mentioning some of the leading types of dentition, reference may be made to one curious adaptive modification connected with food which occurs in the small South African snake known as *Dasypeltis scabra*, which, as stated on page 50, feeds largely upon birds' eggs. On the page referred to it is likewise stated that this snake crushes the eggs upon which it subsists by means of knob-like projections from the spines on the lower sides of the vertebræ of the neck which project into the gullet. Now the button-like extremities of these vertebral spines are furnished with caps of enamel, so that both in structure and function they are comparable to teeth.

Passing on to the consideration of teeth, it may be mentioned that there are three distinct modes in which reptilian teeth are attached to the jaws. Firstly, as in the ichthyosaurs, they may be implanted in a continuous open growth in the jaws; and from this there is but a step, by the development of partitions in the groove, to their implantation in distinct sockets (the codont type), as in crocodiles and the extinct megalosaur. Secondly, there occurs in certain lizards, as well as in the tuatera, what is known as the acrodont type of attachment, that is to say, when the teeth are welded to the summit of the jaws. Finally, we have the pleurodont type, as exemplified in the iguanas, in which the teeth are fused by one side of their bases to the inner side of a parapet formed by the elevation of the outer wall of the jaws. The lizards which exhibit the acrodont type include the stellions (*Agamidæ*) and some of the amphisbænas; while this type reappears in the chamæleons, and as already said in the tuatera.

The socket, or thecodont, type of dentition appears generally associated with carnivorous habits, as witness crocodiles, megalosaurs, pterodactyles, and plesiosaurs; the teeth in all these cases being of a more or less conical (crocodiles) or compressed (megalosaurs) type, although they may become trihedral, as in those specialised plesiosaurs known as pliosaurs. The thecodont type also occurs in the carnivorous, or theriodont, mammal-like reptiles, in which they become differentiated into incisors, canines or tusks, and cheek-teeth, as in mammals. On

the other hand, teeth of a markedly carnivorous type may be implanted merely in an undivided groove, as in the ichthyosaurs, in which their crowns are generally conical and strongly fluted. It seems probable that the thecodont mode of implantation was originally confined to carnivorous forms; the quadrupedal sauropod dinosaurs, such as *Brontosaurus* and *Diplodocus*, in which this mode of implantation occurs, possessing teeth which might have been derived from those of a carnivorous type. On the other hand, it must not be supposed that implantation in sockets, or even in a groove, is characteristic of all carnivorous reptiles, or that implantation in a groove necessarily implies the existence of the latter habits. For instance, in the carnivorous extinct sea-serpents (*Pythonomorpha*) the large and sharp conical teeth were welded to the summits of the jaws in the acrodont fashion; while the teeth of the herbivorous iguanodonts were implanted in grooves.

In connection with the teeth of the sea-serpents, it is important to notice that among lizards and their allies the true acrodont type of dentition is generally associated with carnivorous or insectivorous habits. For example, all the lizards of the family *Agamidae* are carnivorous or insectivorous, as are also the amphisbænas and the chamæleons. The tuatera is also apparently to some extent carnivorous. Perhaps, therefore, it may be safe to assert that the thecodont and acrodont types of dental attachment, and also the implantation in grooves, are to a great extent correlated with carnivorous habits.

On the other hand, it cannot be pretended that the pleurodont type of attachment is correlated with herbivorous habits; for although this type of dental attachment occurs in the herbivorous iguanas, it is equally manifest in the *Lacertidae*, *Varanidae*, and *Scincidae*, most, if not all, the members of which are carnivorous or insectivorous. It is, therefore, difficult to imagine why these two types of dental attachment were evolved. The case of the recent iguanas and of the extinct iguanodonts apparently points, however, to the conclusion that the pleurodont mode of implantation and a peculiar form of tooth are not infrequently correlated with herbivorous habits. For instance, the teeth of the iguanodonts present a certain resemblance to those of the iguanas, while the mode of implantation of the former is only one step from the pleurodont type. Again, the teeth of *Scelidosaurus*

and its allies, which are distant relatives of the iguanodon, are decidedly like those of the iguanas, having compressed crowns with finely serrated edges ; while the spatula-shaped teeth of *Diplodocus*, *Hoplosaurus*, and *Brontosaurus*, which may have been herbivorous, may be compared with *Scelidosaurus*-teeth which had lost their serrations and become spoon-shaped by the pressing-in of one lateral surface. Reverting to the pleurodont type, it may be mentioned that in the family *Scincidæ* the Australian stump-tailed skink (*Trachysaurus rugosus*) will consume vegetable food, such as lettuce ; and, judging from the large flat-crowned teeth, it seems probable that the species of the Australasian genus *Tiliqua* may at times vary their diet with vegetable food, although they appear to be mainly insectivorous.

Be this as it may, it is noteworthy that the teeth of truly herbivorous reptiles are adapted for masticating, and consequently become worn down, this being markedly the case with those of the Galapagos sea-iguana (*Amblyrhynchus*), which feeds on sea-weed, and still more so with those of the iguanodon. Here it may be remarked that, with the possible exception of those of the mammal-like group (Anomodontia), the teeth of reptiles, unlike those of mammals, are replaced irregularly and continuously, the crowns of new ones growing up alongside of or below the old ones as the latter become worn out and useless.

It remains to notice certain types of reptilian dentition which are evidently special adaptive modifications, although it is by no means easy to indicate the object of the adaptation. Firstly, we may notice the rhynchocephalian tuatera, in which, as already mentioned, the dentition is of the acrodont type. Both jaws are furnished with a pair of chisel-like teeth at the front extremity. The edge of the lower jaw is surmounted by a single row of closely crowded teeth ; but in the hind part of the upper jaw there are two parallel rows of such teeth, separated from one another by a longitudinal groove. When in use, the lateral series of lower teeth bites into the groove between the two upper rows ; and when the teeth become much worn away (and there seems to be little replacement), the edge of the upper jaw itself becomes ground down and forms a sharp cutting instrument. The precise use of this complicated arrangement is not apparent. In captivity tuateras greedily devour meal-worms and other insects, but it is believed that vegetable substances form at least

a large proportion of their food in the natural condition. The tuatera is the last survivor of a number of extinct reptiles, specially abundant in the Trias, which exhibit a similar type of dentition, but in some instances in a more intensified form. The most remarkable of these are the pavement-toothed tuateras (*Hyperodapedon*), of which the teeth and jaws are found abundantly in the Triassic rocks of Europe and India. In place of the double row of lateral upper teeth characteristic of the living tuatera, the pavement-toothed species (Fig. 12, B) were furnished with a number of such rows, so that a large portion of the palate was covered with a pavement of bluntly conical teeth, between the outermost and second rows of which worked the knife-like edge of the lower jaw. With the uncertainty existing as to the nature of the diet of the modern tuatera, it would be idle to conjecture what kind of food was consumed by its extinct relative.

Certain other reptiles had a pavement-like dental armature, developed independently of that of the tuatera. In *Endothiodon*, for instance, a member of the dicynodont section of the mammal-like anomodonts, the palate was studded with what look like short and closely approximated pegs. More remarkable still are the bean-toothed reptiles (*Placodontia*), of the Trias, the precise serial position of which is still a matter of uncertainty. These reptiles take their name from the presence of a small number of large flattened teeth covering nearly the whole of the palate, but replaced in the front of the lower jaw by teeth of a chisel-like form. In the typical *Placodus* these teeth are squared, but in the allied *Cyamodus* (Fig. 12, C) they are more rounded, and much resemble the large Australian beans often mounted as match-boxes. Probably these teeth were used for crushing hard substances, such as shells of crustaceans and molluscs.

The poison-fangs of snakes form a connecting link between structural modifications connected with food and those for attack and defence, since those weapons are employed both for killing prey and for attacking enemies or for defending their possessors against attack. Although the most specialised of all venomous snakes, such as vipers and rattlesnakes, differ from most harmless species by their depressed and broad heads (such expansion being chiefly due to the great development of the poison-glands), there is really a gradation from the harmless

to the noxious representatives of these reptiles. Ordinary harmless snakes have, as a rule, two rows of teeth in the upper jaw-bone, or maxilla. In the pythons and boas (*Boidæ*) as well as in the typical section of the family *Colubridæ*, as represented by the English grass-snake (*Tropidonotus natrix*), all the teeth are solid, and these snakes are non-venomous, although the larger kinds are capable of inflicting a severe bite. The section of *Colubridæ* with this type of dentition is known as the Aglypha or solid-toothed colubrines. There is, however, another section termed the Opisthoglossa, or back-fanged colubrines, in which some of the hind maxillary teeth are grooved and connected with a small poison-gland. The group is not a very numerous one, and is best known in the shape of some of the Indian tree-snakes of the genus *Dipsadomorphus*. The poisonous properties of these snakes are not great, but they are sufficient to paralyse the small animals on which these reptiles subsist. Far more venomous are the members of a third group of *Colubridæ*, the Proteroglypha, or front-fanged colubrines, among which are included the deadly krait and cobra as well as the sea-snakes. As their name implies, these snakes are characterised by the circumstance that some of the anterior maxillary teeth are enlarged and grooved or channelled for the conveyance of venom from the poison-glands. The remarkable feature connected with the presence of venom-teeth in the Opisthoglypha and the Proteroglypha is that their development has apparently taken place independently in the two groups.

A third independent development of venom-teeth seems to have taken place in what may be called the typical venomous snakes, namely vipers and rattlesnakes, constituting with their allies, the family *Viperidæ*, although they are really not more poisonous than cobras and kraits. In these snakes the apparatus is of a different nature to that of the venomous *Colubridæ*, for the maxillæ, except for the undeveloped successional ones, only carry a single pair of teeth, which are of such length as to be denominated fangs, and are capable of erection and depression; assuming the erect position automatically as soon as the mouth is opened. These fangs are grooved or channelled for the conveyance of the venom; the grooves or channels are in connection with the ducts of the poison-glands, which are situated on each side of the head, and correspond to the salivary

glands of other animals. A dense fibrous sheath, overlain by a stratum of powerful muscle, invests the poison-gland. When these snakes open their mouths to strike, a special arrangement (into the details of which it is unnecessary to enter) erects the venom-fangs, while at the same time the muscles compress the venom-glands in the same manner as an india-rubber surgical syringe is squeezed by the grasp of the hand, and with such force that when the snake misses its aim or is irritated without having anything at which to bite, the fluid is spurted a considerable distance from the hollow summits of the fangs. The arrangement is perfect, conveying the venom into the heart of the wound; if it had been devised by human skill for killing enemies, it might have been described as a fiendish invention. The nature, properties and effects of snake-poison need not be discussed.

Since the chapter on the food of reptiles was printed off it has been recorded that a viper (*Vipera macrops*) inhabiting Bosnia and Herzegovina feeds almost exclusively on grasshoppers. Although retaining the venom-fangs characteristic of its tribe, this viper, which grows to a length of about 18 inches, is stated to show no disposition to bite when handled, and only attempts to do so when seriously injured. This species is near akin to *V. ursinii* of lower Austria (which, although feeding on lizards and mice, is also stated to show little or no disposition to bite), and thus to the typical viper.

It may be added that the food of the small North American colubrine snakes of the genus *Contia* consists of caterpillars, crickets, grasshoppers, spiders, etc.

Venom-glands and venom-fangs are, however, by no means the exclusive attributes of snakes, at least according to general acceptance, for they occur in the American lizards of the genus *Heloderma*, to which allusion has been already made in connection with colour. These lizards inhabit Central America, Mexico, and Arizona, and are supposed to be represented by two species, one of which is popularly known as the gila monster. Since, however, the two forms differ chiefly, if not entirely, in the matter of colour, it is perhaps permissible to regard them as local races of a single species. These lizards are unique in possessing the power of injecting poison into the wounds made by their teeth in the same manner as venomous

serpents; their dentition being apparently similar to that of the front-fanged colubrine snakes. The anterior teeth are curved and fang-like, and provided with grooves for the transmission of poison secreted by the salivary glands; and, as in most serpents, there are also smaller solid teeth on the palate. As these reputedly poisonous lizards are certainly not the ancestors of snakes, it is evident that their poison-apparatus has been developed independently of that of the latter. The reader will notice that in the preceding sentence the expression "reputedly poisonous" has been employed. Till a short time ago no doubt was entertained that these lizards were venomous, and reports are extant of the serious effects of their bite on guinea-pigs. Recently, however, an American zoologist has thrown doubt on their poisonous properties; although still later the poisonous character of the saliva has been reaffirmed in France.

Venom and venom-fangs are, as already mentioned, connected both with the function of procuring food and with attack and defence, although in most cases mainly with the former; and it would accordingly be appropriate to follow with other defensive and offensive adaptations. Before doing so, however, it is convenient to refer to one remarkable adaptation connected with the procuring of food, namely the tongue of the chamæleon. This organ attains a remarkable development, being capable of protrusion to a distance of seven or eight inches from the mouth. The true tongue is a club-shaped organ, covered with a sticky secretion which retains the victim at which it is projected with unerring aim. This base, or root, on the other hand, is very narrow, and composed of highly elastic tissue. It is supported upon a special process of the hyoid bone, over which it is withdrawn in telescope-fashion; the whole apparatus, while in the contracted state, being comparable to a spring-coil. From the base a pair of elastic blood-vessels and a mass of special elastic tissue extend into the true fleshy tongue. Congestion of the blood-vessels, combined with the action of some of the hyoid muscles, serves to release the spring-like arrangement, with the result that when this occurs (at the will of the creature, or as a kind of reflex action induced by the proximity of food, as the case may be), the thick and club-shaped tongue is suddenly and forcibly shot from the mouth to its full extent. The sticky termination of the club at the same time opens out into an

upper and a lower flap, between which the victim is partially enclosed ; after which, by the action of the elastic tissues of the base the organ is as speedily withdrawn, and the fly or other insect swallowed. Curiously enough, the chamaeleon can only shoot at its prey when at the full distance of seven or eight inches ; the apparatus acting with much less celerity and certainty when the interval to be traversed is much short of this. The process only occupies about a second ; this being the more remarkable when the excessive slowness of the chamaeleon's ordinary movements are taken into consideration.

The first, and at the same time the most extraordinary instance of defensive adaptation that claims attention is a functional one, and occurs in the so-called Californian horned toad (*Phrynosoma cornutum*), to which allusion has been already made in connection with other peculiarities. About twenty years ago an observer in California who happened to catch one of these reptiles was startled to see it suddenly spurt a jet of blood from one eye to a distance of rather more than a foot. On turning the creature over in his hand to examine this eye, its captor was still more astonished to see a jet of crimson fluid spurted from the other eye. The reptile repeated the performance four or five times from both eyes, till the hands, clothes, and gun of its captor were sprinkled with fine drops of bright red blood. When brought into camp about four hours later it repeated the performance three times.

The phenomenon appears to be rarely exerted by these reptiles, in consequence of which doubts have arisen from time to time as to whether it really exists. Testimony recorded by one of the convinced sceptics is of importance as throwing light on the true nature of the phenomenon. An observer who witnessed the action in one of these reptiles so long ago as 1891, conveys the impression that the blood is spurted from the eye itself, an action which it is very difficult to understand. He states, for instance, that on taking a horned lizard in his hand it spurted a little jet of blood from one eye to a distance of about fifteen inches, while when turned round it repeated the action from the other eye. Mr. R. L. Ditmars, after examining some two hundred specimens of these reptiles without noticing the phenomenon, and in consequence having become sceptical as to its existence, had an opportunity of witnessing the mode of action. While

photographing one of these reptiles—an operation which seemed to cause it much excitement—he noticed that the creature suddenly elevated its head slightly, when its neck became rigid, its eyes bulged from their sockets, and a sound was produced like that made by pressing the tongue against the roof of the mouth, and forcing forwards a small quantity of air. This rasping sound, lasting only for the fraction of a second, was accompanied by the emission of a high-pressure jet of blood, which struck the wall four feet distant at the same level as that of the reptile. The emission occupied about one and a half seconds: and the jet of blood, which was as fine as a horse-hair, seemed to issue from the eyelid, which was momentarily swollen. For some time after the eyes remained closed, but when opened they had recovered their normal condition. The quantity of blood ejected was considerable, as no less than 103 spots, averaging an eighth of an inch in diameter, were scattered over the wall: This account renders it clear that the jets do not come from the eyeball itself, and thus removes one difficulty in attempting to account for the phenomenon. Assuming the jets to issue from the eyelid or the corner of the eye, the exact *modus operandi* remains still to be explained.

The following letter from Mr. H. L. Jameson on the spitting powers of African snakes appeared in the *Field* newspaper of 11th January, 1908:—

“The ‘spitting’ habits of certain South African snakes, notably the spij-slange (*Naja haje*) and the ring-hals (*Sepedon hæmachates*), are so well known to colonists that it is strange they should be apparently discredited by many European naturalists. For example, Dr. Gadow, in the *Cambridge Natural History, Amphibia and Reptiles*, p. 632, writing of *Naja haje*, says:—

“‘The name spij-slange, meaning spitting snake, refers to the habit this and other African cobras have of letting the poison drop from the mouth like saliva when they are excited. This is not a particularly economical habit, nor is it of the slightest use to the snake.’

“I had already come across so many persons who declared that these two snakes could not only spit, but could actually project their venom for a distance of several yards, that a practical proof of the habit a few days ago, which might easily have had serious results, was not altogether a surprise.

"Among other snakes in my laboratory on the day in question was a ring-hals, which had arrived in a torpid condition from the Orange River Colony. I transferred this snake to a box about 15 in. deep, with  $\frac{1}{2}$ -in. wire netting over the top, and placed him in a sunny spot. On my return in the afternoon the snake was active and alert, and as soon as I appeared he struck a defensive attitude and spread his hood. After I had passed his box a couple of times, my attention was arrested by his suddenly lowering his head and drawing in a deep breath, after the manner of a puff-adder. I stopped to look at him with my face about 4 feet above his cage; when suddenly, with an upward dart of his head, accompanied by a distinct puff or whiff, he blew a jet of saliva right in my face, some of it entering my right eye. My friend Mr. William Anderson, who was standing beside me at the time, observed the glittering jet of liquid shoot from the snake's mouth. By immediately applying treatment to the eye I got off with nothing worse than slight inflammation, which had almost subsided by the morning.

"A couple of days afterwards I experimented by placing a bell-jar over the wire top of the cage and irritating the snake. As soon as he got excited he blew up a jet of poison each time I approached, which formed a splash of spray on the inside of the jar. The top of the jar was nearly 2 feet from the wire covering of the cage. At each spitting he drew in a deep breath, and blew out the poison with a puff like the spitting noise made by a small cat or mongoose. His aim was, apparently, always directed towards my face, so that by moving my head round to the different sides of the jar sprays of poison were shot on all parts of the glass.

"Two such sprays, each resulting from a single 'spit,' were measured; each consisted of about 150 small drops, distributed in a splash about eighteen to twenty centimetres long and two centimetres wide; the droplets being close together and partly confluent at one end, presumably that corresponding to the point aimed at, and thinning out towards the other end of the splash. Until I had this experience I was inclined to believe that the venom might be merely projected by the rapid movement of the head when the snake tried to strike at an object out of his reach, but I am now convinced that the process is a

true spitting. The phenomenon is so well known here that it would be hardly necessary to publish these observations were it not for the scepticism regarding spitting snakes which still seems to exist at home. I have heard on trustworthy authority of several cases where temporary blindness (probably acute conjunctivitis) resulted from a jet of ringhals or cobra venom in the eye, so that care should be taken in approaching these snakes when in an aggressive mood."

The Gabun viper or river-jack viper (*Bitis gabonica*) may be added to the list of venom-spitting snakes, having been observed to eject its secretion to a considerable distance. One drop ejected into the human eye will cause severe temporary pain or even permanent injury; while dogs are completely blinded when thus struck.

A somewhat analogous, although less remarkable, means of defence is adopted by a North American snake, locally known as the milk-snake (*Ophibalus doliatus triangularis*), which is stated to exude from between its scales a copious flow of an acrid milky fluid. There can be no doubt that the acrid secretion of this snake, like that of the common toad among amphibians is exuded for defensive purposes. The evil smell exhaled from the secretion of certain glands in *Clemmys leprosa* and the "stink-pot" terrapin (*Cinosternum odoratum*) has been already alluded to as a defensive provision; and the habit possessed by certain lizards and snakes of voiding the contents of the cloaca when captured comes under the same category.

As incidentally mentioned in an earlier chapter, the hissing of snakes and monitors, accompanied by rapid vibration of the forked tongue, and frequently by an elevation of the head and neck and the assumption of a threatening or intimidating attitude, seems to be undoubtedly a defensive action. Under the same category may be included the inflation of the hood of the cobra, and the expansion of the neck-frill of the Australian frilled lizard (*Chlamydosaurus kingi*); the latter action being accompanied by the opening of the mouth and the assumption of a threatening attitude. Many, or all, of the iguanas likewise assume threatening or terrifying gestures when approached; the male basilisk, for instance, if it cannot escape detection by crouching down on the branch on which it may happen to be resting, rearing up its head and erecting the crest

on its back in order to terrify the intruder. If these gestures fail to effect the desired end, the reptile throws itself headlong into the water above which it generally takes its station.

Chamæleons when made angry by irritation either present their lateral and broadest aspect to the intruder, or blow out the whole body by inflating it with air, at the same time hissing loudly. Evidently these actions are for the purpose of making the creature appear as large, and therefore as dangerous-looking as possible, and thus striking terror into the hearts of aggressors. The most interesting point connected with these gestures is that the inflation of the body is brought about by means of a special modification in the structure of the lungs, and is therefore an adaptation of deep significance. The lungs of chamæleons, which are very capacious, differ from those of other lizards by the circumstance that, in place of being bag-shaped, they end in a number of narrow blind sacs, which extend far down into the body-cavity, thus permitting the inflation not only of the chest but likewise of the entire body. Whether this peculiar structure of the lungs was developed for the purpose of permitting the periodical inflation of the body, or whether such inflation is a secondary adaptation due to the peculiar structure of the lungs, may be left an open question. In this place may be noticed the peculiar lung-structure of snakes, although it has no connection with either attack or defence, but is merely an adaptation to the long and slender bodily form of these reptiles. The two lungs are unequally developed; the right forming a sausage-like cylinder which extends a long way down the body-cavity, while the left one is a very thin hollow bag of small size, with scarcely any of the usual honey-comb cells in its posterior half or posterior third, so that it merely serves the purpose of an air reservoir and takes no active share in the work of respiration.

Everyone who has had any experience of lizards in the wild condition will be aware that in many species, and even in all the members of certain families, the tail is extremely fragile and apt to snap suddenly in twain when the reptile is startled or seized. The slow-worm (*Anguis fragilis*), for instance, exhibits this peculiar phenomenon to perfection, and takes its specific name from the facility with which it can discard its caudal appendage. When frightened or suddenly seized in the hand, the slow-worm, as well as many kinds of four-limbed lizards,

immediately makes its tail as rigid as a steel-rod ; and while in this condition a slight amount of force is sufficient to cause a complete or partial fracture of this appendage. If the fracture be complete, the tail, when the reptile has been seized, will remain in the hand of the would-be captor, while the lizard itself will run or wriggle off apparently none the worse for the voluntary amputation. When the fracture is incomplete, a transverse crack will be noticed on the under surface of the tail, the upper side of which exhibits no sign of injury. Seeing that a lizard or slow-worm flying from an enemy would more probably be seized by the tail than by any other part, it is obvious that the power of voluntarily separating that member must be a great protective advantage.

In all lizards endowed with this power of tail-amputation the centra, or bodies, of the caudal vertebræ are traversed by a cartilaginous transverse division, or septum ; and it is at one or other of these lines of weakness that the tail snaps. For a long time this was regarded as a satisfactory explanation of the phenomenon ; but it has been pointed out that this is not the cause of the fracture taking place, and in some instances, at any rate, seems to have nothing at all to do with it. Dr. G. B. Leighton, for instance, in his *Life-History of British Lizards*, states that he has observed cases where the fracture took place at the junction of two adjacent vertebræ and not in the middle of one. As the result of observation, coupled with dissection, Dr. Leighton is indeed led to conclude, "that fracture of the tail in the green lizard, as in the slow-worm, depends mainly upon the peculiar arrangement of muscles and integument ; that this fracture takes place, or may do, at definite intervals corresponding to the end of every second caudal scale ; and that this position as regards the caudal vertebræ was at an intervertebral articulation. Given a fracture at any point, one may say with certainty where any other fracture may occur, by simply counting the scales ; the other fractures will be only at the ends of the rows of scales numbering 2, 4, 6, 8, 10, and so on, from the first fractured point. It should be added that the explanation here offered to account for the fragility of the tail is not an accepted view, but it is one which any observant field-naturalist can examine for himself on the first slow-worm he encounters."

This voluntary tail-amputation, as already mentioned, is a defensive measure. Although the regeneration of such lost tails has nothing to do with either defence or attack, it may nevertheless be referred to in this place. Lizards or slow-worms which have thus voluntarily parted with their tails, always grow new ones, although there does not appear to be evidence how often this process of amputation and regeneration may be repeated in the same individual. Not infrequently the new tail is double, or even triple; while occasionally a small extra tail may grow from the spot where the proper tail has been partially fractured. More curious still is the circumstance that in certain cases (although not in the slow-worm and the green lizard and its allies) the scaling of the new tail is of a different type to that of the original one, being simpler, and sometimes at any rate displaying what appears to be the ancestral form. The regenerated tail is indeed but a makeshift affair, for it lacks true vertebræ, being supported merely by an unjointed rod of fibrous cartilage. Nor is this difficult to account for, seeing that the spinal cord could not be renewed, and that it is only around this cord that vertebræ are ever developed. Whether the "bogus" tail is capable of being cast and replaced, history telleth not. As to the length of time required to grow a new tail, it is stated that a pair of geckos which lost their tails at the time of capture grew new stumps nearly half an inch in length after six weeks confinement in a box without food.

The remarkable "rattle" from which the American snakes of the genus *Crotalus* derive their title is an organ whose function is somewhat difficult to determine. Whatever this may be, the apparatus may be appropriately referred to in this place. The rattle forms the termination of the tail in these snakes, and consists of a number of hollow horny structures, somewhat like miniature Swiss sheep-bells, fitting into one another. The terminal bell, which is of course the oldest of the series, is really the horny sheath of the tip of the tail, which was shed but remained attached to the new covering. Similarly each time the skin of the snake is changed, the horny tail-sheath becomes detached, but is retained in position by the new skin, and thus forms the latest addition to the rattle. In course of time as many as a dozen, or, in exceptional cases, even a score, of mov-

able joints or bells may enter into the composition of the rattle. According to an American writer, the general history of the rattle is somewhat as follows:—

"As a snake in its wild state sheds its skin about three times during the warm months, the same number of rattles should be added during the year. To determine the age of a rattlesnake from the number of joints of its rattle is a very uncertain proposition. When the rattle has attained from ten to twelve joints, it usually remains at about that number, as several joints are lost annually through wear. It is only possible to estimate the age of a snake from the number of joints of the rattle when that appendage is of a tapering character and still possesses the 'button' of the snake's birth. The growth of the snake is indicated by such a rattle in the increasing size of each ring from the button to the tail. By allowing three rattles for a year, the reptile's age may be determined with reasonable accuracy. When a snake's rattle possesses all the joints or rings of a uniform size, the snake is old. The tapering portion of the rattle grown in its youth has been lost, together with an uncertain number of succeeding joints, and the snake has ceased to grow.

"These snakes are unable to produce any sound with the rattle until they are about three months old. By that time one skin has been cast, a new joint uncovered on which is attached the 'button' of birth, and a second joint has developed to such an extent that the one preceding it has become dry and brittle. On the latter, the 'button' whirs feebly when the tail is vibrated. In the Reptile House at the New York Zoological Park a specimen of the diamond-backed rattlesnake, now fifteen months old, and born in the building, possesses 'five rattles,' or 'four rings,' and a 'button'. This snake measured fourteen inches at birth. At the present time it measures three feet, six inches. The length of a full-grown diamond-backed rattlesnake is usually about six feet."

Originally it was considered that the rattlesnake was provided with its noisy rattle in order to warn other creatures of its approach, and thus enable them to get out of harm's way. Such a view may, however, be dismissed as childish; and, as Darwin pointed out, it is far more probable that the object of the rattle, like the expanded hood of the cobra and the inflated head of the puff-adder with its accompanying hiss, is to alarm

and terrify such animals as will venture to attack venomous serpents. Some confirmation is afforded to this theory by the circumstance that rattlesnakes, unlike other serpents, do not hiss. The noise of the rattle thus appears to serve the same purpose as hissing ; and if the latter be for the purpose of frightening enemies, the same will clearly be the case with the rattle, which will consequently come in the category of defensive adaptations. It should be observed, however, that the hiss of a snake is regarded by some as a sign of fear and not of defiance, although even then its result is probably the intimidation of enemies. More important is the objection that the sound of the rattle would apparently be quite as likely to attract foes as to disperse them ; and in this connection it may be mentioned that the sound of the rattle of one snake is reported to cause all the rattlesnakes within hearing to set their own apparatus in motion. Another theory, namely that the rattle is for the purpose of attracting noisy insects such as cicadas and grasshoppers within striking distance, by their mistaking the sound of the rattle for the "music" of their own kind, seems sufficiently refuted by the fact that rattlesnakes do not feed on insects.

That the death-feigning instinct, so common among mammals and insects, is not unknown among reptiles, appears to be proved by the behaviour of an American hog-nosed snake (*Heterodon platyrhinus*) described by an American naturalist in 1907. When this snake is alarmed, it flattens its head and neck, puffs out its body, and begins to hiss. Should these intimidating efforts fail to frighten away the enemy another plan is tried. The reptile throws itself into violent contortions, during which the remnants of its last meal are in many instances vomited. After continuing for a few minutes, these writhings gradually diminish in intensity until the snake lies inert on its back, as if defunct. In this posture the reptile may remain from a few seconds to many minutes, the instinct to simulate death being so strongly developed that if the inert body be turned over to the normal position the snake immediately returns to the deadliest attitude at its command. Whenever the spasmodic paroxysms reach the contortion stage, the series of actions is continued to the end. Young snakes usually cease the performance after a few seconds, but old ones will frequently feign

death for ten minutes, while with a little attention they can be induced to remain inert for fully an hour.

This section of the present volume may be brought to a close by reference to a peculiar digestive adaptation artificially produced by certain reptiles. The fact that the marine plesiosaurs of the Oolitic and Cretaceous were in the habit of swallowing pebbles and retaining them in their stomachs for the apparent purpose of assisting digestion, has long been familiar to palaeontologists. Discoveries in America indicate that the great dinosaurs, such as *Brontosaurus* and *Diplodocus*, had a similar habit. The evidence rests on the discovery in two instances of small heaps of polished quartzitic pebbles in association with the skeletons of these reptiles. The pebbles are for the most part bright-coloured jaspers, and bear a polish quite different from that of the ordinary wind-polished or river-worn pebbles found elsewhere in the same beds, so that they are unmistakable. In the one instance about two dozen were found together, but in the second case the number was smaller. Very curious is the fact that each heap included a certain number of bright-coloured fossiliferous jaspers, which are uncommon in the strata, and suggest that the dinosaurs were in the habit of picking out stones of this particular type for swallowing. A further suggestion is that the stomachs of these pebble-swallowing reptiles were furnished with gizzards like those of birds, as it is otherwise difficult to see how the pebbles can have acted efficiently and been permanently retained in the stomach.

It may be added that the stomachs of South American caimans, and probably those of other crodilians, frequently contain balls of hair, derived from the animals upon which they have fed.

## SECTION II

# AMPHIBIA

### CHAPTER I

#### GENERAL CHARACTERS

How distinguished from fishes, and from reptiles. Other general features of structure. Larval development. Classification.

FROGS, newts, and salamanders are mostly small, feeble animals, persecuted by larger and stronger vertebrates of all the other classes, passing part or the whole of their lives in water and when on land lurking in holes or burrowing underground and venturing forth only under cover of the night. With the exception of a poisonous secretion of the skin in some species, as in the toad, they have no means of defence or retaliation, and owe their survival only to their success in concealing themselves and their great powers of reproduction. Formerly confounded with the reptiles, these animals are now distinguished as a separate class under the name Amphibia, which refers to the fact that they are not merely amphibious in the popular sense, living partly in the water and partly on land like the hippopotamus, but that they are actually adapted in the earlier period of life to breathe in water by means of gills, like fishes, and in the later period to breathe air by means of lungs, like reptiles. A frog is in fact in its tadpole condition physiologically a fish and in the adult condition physiologically a reptile. There are, however, some Amphibia which never lose their gills, and some which on the other hand never breathe water in their immature condition; and therefore the class cannot be completely distinguished by these physiological adaptations. The term Amphibia is thus not always appropriate, and some zoologists, like Dr. Boulenger, prefer the name Batrachia for the whole class. The most important difference between Amphibia and fishes is in the organs of locomotion:

the paired limbs of fishes are *fins*, fan-like structures of which the skeleton consists of rays radiating from the girdles to which they are attached, while those of Amphibia, like those of all terrestrial vertebrates, are *legs*, jointed cylindrical structures resembling fins only in their terminal parts, the feet, which are supported by five rays termed the digits. The terrestrial limbs have been described as tetrapodous and pentadactyle, but neither of these epithets is particularly appropriate; tetrapodous merely means four-footed and the number of limbs is the same in fishes, while pentadactyle, although it expresses a general characteristic of the terrestrial limb, refers only to the foot or terminal portion which is most similar to the fin of a fish. More appropriate terms to express the conditions to which the two types of limb are adapted, and thus indirectly their structure, would be *hydrobatous* or going in water, and *geobatous* or moving on land. The fin of the fish has also been termed the ichthyopterygium, and the leg of terrestrial vertebrates the cheiropterygium, terms which mean fish-limb and hand-limb, but the latter term is obviously inaccurate as the word hand does not suggest the leg of an animal. The important fact is that there is an essential difference in structure between the limbs of fishes and those of terrestrial vertebrates and this difference is as well indicated by the English words fin and leg as by any others. Many Amphibia during part or all of their lives possess median unpaired fins, but these are never, like those of fishes, supported by skeletal fin-rays.

These differences distinguish the Amphibia from fishes but not from other classes of terrestrial Vertebrates. From these they are completely separated by the absence of the amnion in the embryo and the absence of the allantois—an outgrowth of the hind-gut of the embryo which absorbs oxygen, and thus serves instead of a lung during embryonic development. The allantois cannot be said to be entirely wanting, for the urinary bladder of the Amphibia seems to be its representative; but this bladder has nothing to do with the respiration of the embryo. These differences however are of little use in distinguishing adult specimens. All existing Amphibia differ from reptiles in the absence of horny epidermic scales or scutes, and in the presence of glands which render the skin soft and moist; in the order Apoda or limbless Amphibia dermal scales are

present as in fishes and many reptiles. The absence of epidermic scales does not apply to the extinct Amphibia called Stegocephali or Labyrinthodonts, and thus neither the epidermis nor the derma affords a completely diagnostic character.

There are, in addition to the above, many peculiarities of internal structure in Amphibia which must be briefly described. The skull articulates with the vertebral column by two distinct condyles, a terrestrial character in which they differ from fishes where there is no movable articulation at all, and from all the higher classes except mammals—reptiles and birds having only a single condyle. Huxley regarded this similarity between Amphibia and mammals as indicating that the latter sprang directly from the former, but later discoveries show that the mammals are descended from primitive reptiles. Like fishes the Amphibia in the aquatic larval stage possess sense-organs in the skin of the head and of the sides of the body, forming in the latter position not one lateral line but two or more; the organs are on the surface not enclosed in tubes. After the metamorphosis the organs become covered by epidermis, and in the Anura disappear altogether, but in some Urodela they are found again on the surface of the skin when the animals return to the water in the breeding season. With regard to the gill-slits they resemble those of fishes and are separated by similar gill-arches; the number however is reduced to four, not including the spiracle; the external gills which are developed on the first three gill-arches are similar to those of larval lung-fishes and *Polypterus*. In the tailed Amphibia or Urodela the gill-slits are never covered by an operculum, and no internal gills are developed, but in the tail-less forms or Anura, such as the common frog, the gills first formed disappear and other smaller gill-processes are developed on the arches which are then enclosed by the operculum or gill-cover. Formerly these enclosed gills were called internal gills and supposed to be homologous with those of fishes, but according to Dr. Gadow they are really developed on the exterior of the arches and are of the same nature as the original external gills.

The lungs, like those of *Polypterus* and the lung-fishes, are a pair of sacs arising by a single ventral aperture from the pharynx or throat, immediately behind the gill-slits; they project freely into the abdominal cavity. In typical cases the gill-

slits close up during the metamorphosis and the lungs become the chief organs of respiration, supplemented by the skin which being moist and richly supplied with blood takes part in this function; and it is a most extraordinary and remarkable fact that in some cases, both lungs and gills degenerate and the skin is the only organ of respiration. Ribs being small or reduced to mere vestiges, air is forced into the lungs by the compression of the mouth cavity and expelled by the elasticity of the lungs and body walls. The original single aperture of each nasal sac, as seen in Elasmobranch fishes, is divided by the maxillæ and pre-maxillæ into two, an external nostril on each side of the surface of the snout and an internal nostril in the roof of the mouth cavity. Air is taken in through the nostrils while the mouth is closed, and the external nostril is closed by muscular action when the air is forced into the lungs.

In the larval or tadpole condition the heart and branchial, or gill, arteries, have a structure and arrangement similar to those of fishes. The heart has a single auricle and a single ventricle, the former receiving the blood from the veins and passing it into the ventricle, which pumps it through the gills, into all parts of the body. After the metamorphosis, when the animal is adult and possesses lungs, the auricle is divided into two, the right receiving the blood from the body, and the left the blood from the lungs. The ventricle, however, remains single, both auricles opening into it, so that a certain amount of mixture of the blood from the body and that from the lungs takes place, as in reptiles.

The existing members of the class consist of three obviously distinct groups the characters of which are conspicuous, and between which there are practically no intermediate forms. These three groups are the well-known and abundant tail-less jumping forms like the frogs and toads, the tailed walking forms like the newts and salamanders, and the small group of burrowing Amphibia which are entirely destitute of limbs and are confined to the tropics. These groups form three Orders called the Anura (meaning tail-less), the Urodela (meaning with persistent tails), and the Apoda (meaning leg-less). Of these the Urodela or newt-like forms are, if not in all respects the most primitive, the least specialised, and will therefore be considered first. The extinct Labyrinthodonts form a fourth group regarded by Dr.

Gadow as a sub-class equivalent to the other three orders taken together as forming a separate sub-class. The former he names the Phractamphibia from *phraktos*, armoured, because they possessed calcified or ossified scales embedded in the skin resembling those of primitive fishes, and probably covered externally by epidermic cornified scutes. The second sub-class he names Lissamphibia from *lissos*, smooth. We shall consider the Labyrinthodonts in relation to the evolution of the Amphibia and proceed here to describe the subdivisions of the three Orders of existing forms.

#### I. URODELA.

In the members of this order the primitive elongated form of the body is retained as in lung fishes and in lizards, the trunk being continued without any sudden change of shape into the tail or post-anal region. The tail in the adult continues to serve, as in the larva, as a swimming organ when the animal is in the water. The limbs are somewhat small, usually pentadactyle, but in many genera the number of digits and the size of the limb are reduced. The pelvic or hip-girdle is transverse to the vertebral column, not extended obliquely backwards as in Anura; ribs are better developed than in Anura; the skull is not so much reduced, retaining more separate bones. The tongue is much less developed than in the Anura, and in some of the perennibranchiate or persistent-gilled forms is rudimentary. With regard to the condition of the gills, the gill-slits or clefts must be distinguished from the gill-processes. In the Proteidæ and Sirenidæ the latter persist throughout life, while in the Amphiomidæ the gill-processes always disappear in the adult condition, but one pair of clefts in some species remains open. The operculum is vestigial, never completely covering the gills or clefts.

The Order is divided into four families: the Salamandridæ, Amphiomidæ, Proteidæ and Sirenidæ. Of these the first is the most highly developed and most terrestrial in the adult state.

SALAMANDRIDÆ: *Newts and Salamanders*.—These have no gills or clefts in the adult. Both jaws are furnished with teeth and the eyes are protected by movable lids. Fore and hind limbs are present, but sometimes reduced. This family

has been divided into four sub-families differing in the arrangement of the teeth on the palate and in the structure of the vertebræ. One of these sub-families, the Salamandrinæ, is almost entirely confined to Europe and northern Asia, which form what is called the Palæarctic region. The two principal genera of this division are *Triton*, also called *Molge*, which includes the familiar and abundant newts, and *Salamandra* which contains the salamanders. The two genera differ in certain characters of the teeth and skull, but can be easily distinguished by external characters and habits. The newts are much more aquatic than the salamanders and in accordance with this difference the tail of the former is compressed from side to side and in most species furnished with a fin-membrane, while in the salamanders the tail is round and destitute of a fin. Newts spend a considerable part of the year in the water in the breeding season, and at this time the males usually develop a fold of skin or crest along the back. There are only three species of *Salamandra* and none of them occurs in the British Isles. They are much more highly coloured than the newts, the spotted salamander, *S. maculosa*, being black with large bright yellow patches, the Alpine salamander, *S. atra*, uniformly black. The newts are usually of a mottled brown colour above, but the males, especially in *T. cristatus*, develop bright orange colour with black spots on the belly. Both the spotted and the Alpine salamander are viviparous, but the newts lay eggs. Three species of *Triton* occur in England : *T. vulgaris* or *punctatus* is the common newt ; it is distinguished by its black spots and by the crest in the male being undulated but not notched ; it is continuous with the tail fin. The larger crested newt, *T. cristatus*, is blotched or marbled, not spotted, and the crest of the male is high and notched or serrated along its edge ; it is separate from the caudal fin. (See Plate XIII., A, B.) Adults of this species are five to six inches in length while *T. vulgaris* seldom exceeds three inches. The third species is *T. palmatus*, the webbed newt ; it does not exceed three inches, is of olive-brown colour and in the male the hind toes are fully webbed. Numerous other species occur in Europe, one of the most curious of which is *T. waltlii*, of the Spanish peninsula. This species is very aquatic and has a tail fin-membrane but there is no crest on the body in the males ;



CRESTED NEWT (*MOLGE CRISTATUS*), MALE



DITTO, FEMALE



BULL-FROG (*RANA CATESBIANA*)



the ribs are very long and pointed and frequently perforate the skin.

The sub-family *Amblystomatinae*, which includes the celebrated axolotl, consists of seven genera distributed through North America, Mexico, and Northern Asia from the Ural Mountains to Kamtchatka, Japan, China, and Siam. The largest genus is *Ambystoma*, of which sixteen species are North American and one occurs in Siam; the Mexican axolotl is the sexually mature larval form of *A. tigrinum*, a species which occurs from New York to California and Central Mexico.

FAM. AMPHIUMIDÆ.—Gill-processes are absent in the adult, but except in the huge Japanese Giant Salamander, *Cryptobranchus japonicus*, one pair of gill-clefts persists, namely the last pair, or occasionally only the one of the left side. Maxillary bones are present, teeth in both jaws and in transverse rows on the vomers. The vertebræ are amphicœlous—concave at each end. Both pairs of limbs are present but the eyes are small and without eyelids.

There are only three species in this family. The three-toed salamander, *Amphiuma means* or *tridactyla*, is about three feet long and lives in swamps and the ditches of rice grounds in the south-eastern States of North America. (Plate XIV., B.) The fore and hind limbs are small, and far apart, ending in three small toes; the tail is short. The small gill-cleft on each side is

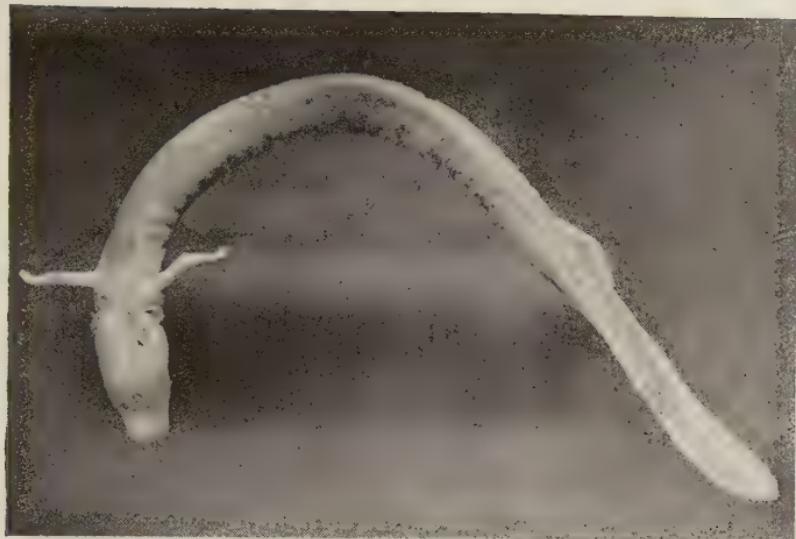
st in front of the fore limbs. The North American "Hell-vender" *Cryptobranchus* or *Menopoma alleghaniensis*, which lives in the rivers of the mountainous regions of the eastern States of North America, is shorter than *Amphiuma*, not exceeding eighteen inches in length, but is much stouter and broader with longer tail, more similar to an ordinary newt; the limbs are also more developed with four toes on the fore-foot, five on the hind. The tail is fringed with a fin-membrane. The skin is very glandular and projects into a thick undulating ridge along the sides of the body. *Cryptobranchus japonicus*, the giant salamander of Japan, lives in that country and in China in mountain streams, hiding in holes or burrows; it reaches the enormous length of four or five feet. The gill-slits are all closed. It is apparently very long-lived since in captivity a specimen lived for fifty-two years.

FAM. SIRENIDÆ.—The members of this family have three pairs of fringed, external gills, retained throughout life. A long and slender body, hind limbs wanting, fore limbs short, with three or four fingers. Maxillary bones absent; small teeth on the vomers, jaws without teeth, and covered with horny sheaths. Eyes small, without lids.

There are only two species, both found in the south-eastern States of North America. In the "mud-eel" (*Siren lacertina*) there are three gill-clefts, the first of the original four being closed. (Plate XIV., C.) The animal reaches a length of two and a half feet; the tail, about one-third of the total length, is compressed and furnished with a fin-membrane. The early development is unknown but it has been shown that in young specimens the gills are small and functionless so that they are redeveloped in the adult. In *Pseudobranchus striatus* there is only one pair of gill-clefts and the gills are covered by the skin, and functionless. There are only three fingers and the length of the adult is not more than seven inches.

FAM. PROTEIDÆ.—The few species placed in this family resemble the Sirenidæ in all respects except in the absence of the hind legs and of teeth in the jaws; in the Proteidæ teeth are present in both the upper and the lower jaw and both pairs of limbs are present. The eyes are without lids. Three pairs of external gills persist throughout life, but there are only two gill-clefts on each side, the first and last being closed up.

*Proteus anguinus*, known in German as the Olm, is a blind and colourless species living in the underground waters of the caves of Dalmatia. (Plate XIV., A.) The limbs are small and slender with three fingers on the fore-foot and two on the hind. The tail is compressed and provided with a fin-membrane. The eyes are rudimentary and concealed beneath the skin. The total length is less than one foot. *Necturus maculatus*, which has also been named *Menobranchus lateralis*, is similar to *Proteus* and of about the same size, but it is pigmented and the eyes are functional; it has four toes on each foot. It lives in North America to the east of the Mississippi and in the Canadian lakes. *Typhlonolge rathbuni* is a subterranean form like *Proteus*, white and blind; it has four toes on the fore-foot, five on the hind. This animal is only three inches in length and has a deep fold of skin on the throat formed of the united opercular flaps.



*PROTEUS ANGUINUS*



*AMPHIUMA MEANS*



*SIREN LACERTINA*



The only known specimens were obtained in the water from an artesian well near San Marcos in Texas.

## II. ANURA, TAILLESS AMPHIBIANS OR BATRACHIA SAVENTIA.

This is the largest Order of existing Amphibia, containing about 900 species, and the differences between them are somewhat slight. They are divided into three sub-orders: (1) the Aglossa, in which the tongue is absent; (2) the Arcifera, in which the two halves of the pectoral girdle are not united together but overlap one another; (3) Firmisternia, in which the halves of the pectoral girdle are united together by cartilage. These two divisions of Batrachians with well-developed tongues are typified by the toad and the frog. The Hylidæ, usually called tree-frogs, are really allied to the toad.

### SUB-ORDER FIRMISTERNIA.

This sub-order contains only two families, the Ranidæ or common frogs, and the Engystomatidæ or narrow-mouthed frogs.

FAM. RANIDÆ.—*Rana temporaria* is the common English frog, which is equally common on the continent; it is also called the brown frog or grass frog. The male has two vocal sacs of the kind called internal, that is to say they are entirely covered by the skin which is simply distended by them when they are inflated. The male has also a swollen pad of skin on the inner side of the first finger which becomes enlarged and black in the breeding season. The habits are distinctly terrestrial, the animals only seeking the water in order to breed. *Rana esculenta*, the edible frog of the continent, reaches a larger size and is distinguished by the following characters: the toes are webbed to their extremities, the vocal sacs are external and there is a prominent glandular patch of skin behind the eye. The habits of this species are much more aquatic than those of *R. temporaria*, and it is never found far from water, into which it always retreats when alarmed. This species is not a native of the British Isles, but it was formerly found in Cambridgeshire and is now abundant in some parts of Norfolk. Specimens are known to have been imported from France and Belgium and turned loose in recent years, and they were probably imported

in former times by the monks of Lombardy. The edible frog croaks much more than the common species; the latter only does so individually and occasionally, but edible frogs are gregarious and they croak in concert, often the whole night long.

*R. catesbeiana*, formerly known as *R. mugiensis*, is the bull-frog of North America; it reaches a length of five to seven inches with hind-legs nine or ten inches long. (Plate XIV., C.) The tympanum in this species is very large and the voice loud enough, when uttered by hundreds of males in a pond, to be heard half a mile off.

#### SUB-ORDER ARCIFERA

FAM. BUFONIDAE.—In this family there are no teeth in either jaw, no ribs, and the transverse processes of the sacral vertebræ are dilated. The genus *Bufo*, like *Rana*, is large, containing more than a hundred species which are distributed all over the world except Australasia and Madagascar. The tongue is free behind but not bifurcate; the toes of the fore-foot are free, those of the hind-foot more or less webbed. The skin always contains numerous poison glands which are concentrated in thickened swellings behind the ear. The rough warty character of the skin in the common species is not universal, in some it is smooth and moist, in others again covered with dry, horny spikes. The common toad, *B. vulgaris*, has a warty skin and sometimes minute cornified spines also. (Plate XV., C.) The female is from three and a half to five and a quarter inches in length, the male somewhat smaller. The male has no vocal sacs and has slighter nuptial excrescences than the frog; they breed like the frog in the water and the eggs are distinguished by forming strings instead of irregular masses.

The Natterjack toad, *Bufo calamita*, occurs in Ireland where the common toad is absent.

The sub-order includes four other families, namely Pelobatidæ, burrowing toads, Discoglossidæ with tongue attached by its whole base, Hylidæ, the tree-frogs, and Cystignathidæ.

#### SUB-ORDER AGLOSSA

This sub-order is not divided by Dr. Gadow into families. The tongue is absent, the Eustachian tubes, conducting air from the mouth to the middle ear, open by a single aperture in the





SMOOTH-CLAWED TOAD (*XENOPUS LAEVIS*), DORSAL ASPECT



SAME, VENTRAL ASPECT



COMMON TOAD (*BUFO VULGARIS*)

posterior part of the palate, the tympanic cavities are wide but the tympanic membrane is not distinct from the rest of the skin. The second, third and fourth vertebræ carry long ribs. The two halves of the pectoral girdle meet and partly unite in the middle line. The Aglossa have been regarded as very primitive Anura but according to Gadow they have few primitive characters, such as the ribs and the presence in the tadpoles of paired opercular apertures; most of the characters are specialisations in adaptation to an aquatic mode of life, the original evolution of the Anura having been due to adaptation to terrestrial life. *Xenopus* or *Dactylethra* is a genus with several species confined to Africa. It is distinguished by a small tentacle below the eye, a row of apertures of cutaneous tubes along each side of the dorsal surface, tubes probably similar to the dermal sensory tubes of tadpoles and fishes, and claws on the first three toes of the hind-foot, all the toes of this foot being fully webbed. The clawed toad, *Xenopus laevis*, is entirely aquatic in its habits. (Plate XV., A, B.) It lives well in captivity and the tadpoles have been hatched in England. The tentacles begin to sprout out on the sixth day after hatching and grow to a considerable length becoming much reduced during the metamorphosis. It is possible that these tentacles are homologous with, or answer to, organs called balancers which are developed above the angle of the jaw in the larvæ of Triton, *Amblystoma*, and other Urodela, and with the tentacular organs of the Apoda. The only species of the Aglossa in South America is the celebrated Surinam Toad, *Pipa americana*. In this creature the head is depressed and triangular, the eyes very small, cutaneous flaps are situated on the upper lip in front of the eye and at the angles of the mouth; the skin is covered with small pointed tubercles, the toes of the fore-foot are slender and free, terminating in star-shaped tips, those of the hind-foot are fully webbed. The eggs are embedded in the skin of the back of the female, and the young pass through the whole of their metamorphosis in this position.

### III. APODA, OR LIMBLESS AMPHIBIA

This order includes a small but remarkable group of limbless, elongated Amphibia known as Cæcilians, or Gymnophiona, which live and burrow in the soil like earthworms;

and are confined to the tropical regions of South America, Africa and India; none are found in Madagascar or Australia. The tail is very short. The skull differs considerably from that of other existing Amphibia and shows resemblances to that of the extinct Stegocephali or Labyrinthodonts. The bones are much broader and more solid than in other Amphibia, the whole skull being firm and compact. The vertebræ are very numerous, in some species more than 200; there is no trace of the skeleton of the limbs or limb-girdles, or sternum. Most of the vertebræ carry rather long ribs, which do not meet ventrally. The eyes are reduced to mere vestiges, and functionless, either concealed under the skin or even beneath the jaw-bones. The sensory organs which compensate for the want of eyes are the facial tentacles, each of which is flat or globular, not long, and is attached to the base of a pit between the eye and the nostril; it is protruded by being distended with blood, like an erectile organ, and is retracted by a strong muscle. There is a large gland whose secretion is discharged into the sac of the tentacle. In many genera, but not all, the skin contains calcified scales. The epidermis is continuous, but the deeper-lying derma is in two layers bound together by transverse lamellæ in successive annular lines; each compartment so formed contains glands anteriorly and scales posteriorly.

The following table shows the relations of the principal divisions of the existing Amphibia:—

CLASSIFICATION OF EXISTING AMPHIBIA.

ORDER.	FAMILY.	SUB-FAMILY.	REMARKABLE SPECIES.
Urodea.	Salamandridæ (Newts and Salamanders).	1. Salamandrinæ.	Salamandra maculosa, Spotted Salamander. S. atra, Alpine Salamander. Triton cristatus, Crested Newt. T. vulgaris, Common Newt. T. palmatus, Webbed Newt.
		2. Amblystomatinæ.	Ambystoma tigrinum, the larva of this species is the celebrated Mexican Axolotl.
		3. Plethodontinæ.	Speleotes fuscus, the only European species.
		4. Desmognathinæ.	Typhlotriton spelaeus, a blind cave-newt in Missouri.

ORDER.	FAMILY.	SUB-FAMILY.	REMARKABLE SPECIES.
Urodela.	Amphiumidæ Gills absent, but one pair of gill-slits usually pre- sent in adult.		Amphiuma tridactyla, Three- toed Salamander. Cryptobranchus alleganiensis, the Hellbender of the United States. Cryptobranchus japonicus, the Japanese Giant Salamander.
	Sirenidæ Hind limbs wanting. Three pairs of external gills through- out life.		Siren lacertina.
	Proteidæ Three pairs of gills, two pairs of gill- clefts, hind limbs pre- sent.		Proteus anguinus, blind, lives in caves of Dalmatia. Typhlonolge rathbuni, also blind and subterranean, in Texas.
Anura. 1st Sub-order. Firmisternia.	Ranidæ Frogs.		Rana temporaria, Common Frog, British. R. esculenta, Edible Frog. R. catesbeiana, Bull Frog of North America. Rhacophorus and other genera are tree-frogs with discs on the toes.
2nd Sub-order. Arcifera.	Engysto- matidæ.		Rhinoderma darwinii, carries eggs in its vocal sacs.
	Bufonidæ Toads.		Bufo vulgaris, Common Toad.
	Pelobatidæ.		Pelobates fuscus, Spade-foot Toad.
	Discoglos- sidæ.		Bombinator igneus, Fire-bellied Toad. Alytes obstetricans, Midwife Toad.
	Hylidæ Tree-frogs.		Hyla arborea, Common Tree- frog of South Europe. Nototrema, the Marsupial Frog.
	Cystigna- thidæ.		Pseudis paradoxa. Ceratophrys ornata, Horned Toad.
3rd Sub-order. Aglossa.			Xenopus laevis, the Clawed Toad. Pipa americana, the Surinam Toad.
Apoda. Limbless.	Cœciliidæ.		Ichthyophis glutinosa.

## CHAPTER II

### EVOLUTION AND GEOLOGICAL HISTORY

The earliest Amphibia, the extinct Labyrinthodonts. Absence of transitional forms in the Secondary Formations. Number of Amphibia in comparison with other classes.

**I**N considering living Amphibia only, the forms which belong to the fauna of the present period of the earth's history, we naturally come to the conclusion that the aquatic larval stage with its gills and gill-clefts retains the characters of the fish-like ancestor, and that the metamorphosis repeats with little alteration the original changes by which the fish became adapted to a terrestrial and air-breathing mode of life. In accordance with this view zoologists formerly regarded those Amphibia which retain the organs of aquatic respiration most completely in the adult condition as the most primitive, and least modified from the condition of the fish-like ancestors. Thus the Proteidæ and Sirenidæ as well as the Amphiuridæ would be the least modified Amphibia showing most perfectly the ancestral characters, while the Anura and the Apoda would be the most recent modifications and specialisations. Before accepting such views, however, we must inquire whether they are confirmed or contradicted by the evidence of palæontology and ascertain whether the Amphibia which existed in earlier geological periods really resembled the perennibranchiate forms of the present day; we must consider what has been the geological history of the Class.

The earliest known terrestrial vertebrates provided with two pairs of five-toed, obviously terrestrial limbs (p. 158), are the animals known from the structure of the teeth in some of the most typical forms as Labyrinthodonts, from the bony covering of the head as Stegocephali. In studying the remains of the skeletons of these extinct vertebrates the

question arises whether they can be distinguished from reptiles, especially from the reptiles of the same or slightly later periods. It is impossible to avoid the conclusion that the existing Amphibia as well as the earliest reptiles were derived from the Stegocephali : the latter are distinguished by the possession of two occipital condyles or none at all, by the structure of the vertebræ, and by the primitive characters of the skeleton to which that of the Apoda and Urodela is evidently allied. It is usually stated that the whole of the dorsal surface of the skull is covered or roofed over by dermal bones, which means that in these primitive Amphibia the flat or membrane-bones of the skull were still in the condition of dermal scutes, as in the primitive bony fishes such as the African fish *Polypterus* and the lung-fishes. Dermal bones, or scales, were also present in many types of the group on the body, either on all parts or only on the lower surface, but some were destitute of such structures. The fossil skeletons naturally do not throw much light on the condition of the gills or lungs, but in the Branchiosauri, one of the sub-orders, representatives of which are found in the Carboniferous and Permian formations, the young specimens show very distinct gill-arches with numerous nodules and denticles on them ; there can be little doubt that these arches carried functional gills like those of the aquatic larvæ of existing Amphibia. *Branchiosaurus salamandroides* is found abundantly in the Permian beds of Europe and specimens are found of almost every size and stage of development from larvæ of three-quarters of an inch to adults of two and three-quarter inches. Gill-arches and gills seem to be absent in the adult so that in all probability this form at least went through the characteristic Amphibian metamorphosis. In the Carboniferous strata are found skeletons of another sub-order in which the body was long and snake-like, without any limbs ; in these gill-arches have been recognised behind the head and these carry skeletal rods supposed to have been the supports of external gills which were retained throughout life ; it has been suggested that these were the ancestors of the existing Apoda, but no connecting forms from intermediate periods are known. In the Carboniferous are also found *Keraterpeton* and *Urocordylus*, animals shaped like a newt, with a ventral armour, and about a foot in

length ; these had terrestrial limbs but traces of gills or gill-arches have not been found in them.

In another Order of Stegocephali we have *Archegosaurus*, represented by many well-preserved skeletons which reach a length of four or five feet. These have well-developed terrestrial limbs with four toes in front and five behind ; the enamel of the teeth is much folded in the Labyrinthodont fashion ; young specimens show traces of gill-arches and the surface of the bones of the skull is marked with grooves which probably contained dermal sense-organs like those of fishes. *Archegosaurus* occurs in the lower Permian of Germany. The third Order of the sub-class, called *Stereospondyli*, contains the most highly developed Stegocephali ; *Labyrinthodon* itself is one of the latest genera ; it occurs in the Upper Trias of Warwickshire. Some of these creatures were of gigantic size ; the largest called *Mastodonsaurus*, from the Trias of England and Germany, had a skull which was nearly a yard in length. No evidence of young or larvae with gills has been obtained in connection with these later Labyrinthodonts.

Transitions from these ancient Amphibians to the modern forms now existing have not yet been discovered. The Labyrinthodonts seem to have become extinct at the end of the Triassic period, and scarcely any Amphibian fossils are known from this period to the beginning of the Tertiary. That such remains should not occur in the great thicknesses of the marine deposits such as the Oolite and the Chalk is not surprising, but it is difficult to account for their absence from the fresh-water deposits of the Purbeck and Wealden beds. In the Purbeck beds are several fresh-water strata with remains of fresh-water shells, mammalia, trees, and land plants. There is evidence that the ancient forest soil with its vegetation was slowly submerged by fresh water, forming for a time at least a shallow lake or marsh, and furnishing it would be supposed ideal conditions for Amphibian life ; and yet these deposits have revealed no Amphibian skeletons. As the Purbeck beds form the uppermost strata of the Jurassic formation so the Wealden are the lowest of the Cretaceous ; in ascending order the Wealden deposits come next to the Purbeck. The lower layers of the Weald clay and the Hastings sands beneath it contain abundant evidence of fresh-water conditions, namely

fresh-water Molluscs and Crustacea, such as *Paludina* and *Cypris*; they also contain remains of terrestrial plants and of *Iguanodon*, a terrestrial reptile. In the Wealden strata of Belgium has been found one little skeleton named *Hylæobatrachus croyi* which belongs to the Amphibia; it is in all probability directly ancestral to some of the existing Urodela, resembling the Proteidæ except that it has maxillary bones and five toes on the hind limb. In the later strata of the Cretaceous series, mostly marine, no remains of Amphibia have been found. In the Oligocene of France, intermediate between the Eocene and Miocene, mere fragments described as *Megalotriton* occur, and in the lower Miocene other fragments have been found which seem to belong to the genus *Triton*. In the Upper Miocene of Oeningen in Switzerland was found the celebrated *Andrias scheuchzeri*, an almost complete skeleton about three feet in length described in 1726 by its discoverer Scheuchzer as 'homo diluvii testis,' the man who witnessed the deluge. Cuvier recognised this skeleton as that of some large newt, and modern palæontologists have ascertained that it is scarcely to be separated from the genus *Cryptobranchus* now existing in America and Japan. The existing common newt, *Triton cristatus*, has been identified in the Norfolk forest-bed which is earlier than the oldest deposits of the glacial period.

Palæontology affords no more light upon the evolution of the leaping Batrachia than on other difficult problems connected with the Amphibia. Intermediate forms, between the Urodela and the Anura, though they must have once existed, have not yet been discovered. Of fossil forms one of the best known is *Palæobatrachus* which occurs in the Lower Miocene; numerous specimens have been obtained and more than a dozen species distinguished. This genus is allied to the Aglossa, which have some primitive characters, but in many others are very highly specialised. The typical forms *Rana* and *Bufo* have been discovered in the Upper Eocene and the earliest representatives of the Anura are still to be sought in formations earlier than this.

It will be seen then that the geological record, imperfect as it is in many respects, seems to contradict one conclusion which was formerly generally accepted, namely that the most primitive Amphibia are those which retain their gills or gill-clefts throughout life. It is now evident that the retention of the

aquatic respiratory organs is no evidence of primitive character. The reasons which lead to this conclusion are of three kinds, palæontological, anatomical, and bionomical, that is those connected with the life-histories of certain forms. Palæontologically there is reason to believe that the Palæozoic Stegocephalia were the ancestors of all the later Amphibia, and in these the evidence goes to show that gills were present in the young but not in the adult condition. Secondly the peculiarities of the limbs are obviously adapted to terrestrial progression and could not have been evolved except in response to the needs of an animal that walked on the ground, while on the other hand a terrestrial animal could not breathe by gills. In fishes the pelvic girdle and limb are smaller than the pectoral and the pelvic girdle is not attached to the vertebral column; in Amphibia the hind limbs when well developed are the larger and the pelvic girdle is attached to the vertebral column. Thirdly we know from numerous observations and experiments that the larval stage of Salamandridæ and Anura may under unusual conditions be prolonged, and the animal may even become sexually mature in the aquatic larval state, as is normally the case with the axolotl in the lakes of Mexico. It is most probable therefore that the retention of gills in existing Amphibia is due, not to the persistence of an ancestral condition, but to a retention of the aquatic habits and larval characters in forms descended from ancestors which were entirely gill-less and terrestrial when adult. It must be borne in mind however that even in the Carboniferous period there were Labyrinthodonts, namely the Aistopoda, which had no limbs and which are believed by some authorities to have had external gills throughout life. It has been suggested that the modern Apoda (p. 167) which in structure of skull and the possession of dermal scales most resemble the Labyrinthodonts, are directly descended from these ancient limbless forms. The resemblance of the Aistopoda, however, to other Labyrinthodonts in the skeleton indicates that they are themselves derived from terrestrial forms provided with limbs. Another important point is that some of the Labyrinthodonts such as *Archegosaurus*, have definitely arranged grooves on the bones of the head which probably contained in life sensory tubes like those of fishes; this is an indication of strongly aquatic habits but not necessarily of aquatic breathing, for such

sense-organs are present in newts during the breeding season when they live in the water.

Dr. Gadow reconstructs the stages in the evolution of Amphibia as follows:—

(1) Terrestrial with two pairs of limbs with five toes on each, breathing by lungs only, with five pairs of gill-arches, which during embryonic life perhaps carried internal gills; with or without several pairs of gill-clefts.

(2) External gills were developed in the embryo, i.e. before hatching, and were afterwards retained later during larval life; these external gills superseded the internal gills of which there are now no traces in Urodela or Anura (p. 159).

(3) Some Urodeles, prolonging the aquatic life, retained and enlarged the external gills into more or less permanent organs.

(4) Some Urodela, e.g. *Salamandra atra*, have become entirely terrestrial, the larval metamorphosis being passed through in the maternal oviduct. The possession of unusually long external gills by this species and by Apoda indicates that these organs are essentially embryonic, not larval features.

The present writer is unable to agree with these conclusions entirely. The presence of external gills in the larvæ of Polypterus and the lung-fishes among fishes, from which the Amphibia were derived, indicates that these organs were probably already present in the larval stage of the earliest Amphibia. The special elongation of the external gills in the embryos of Apoda and in those of *Salamandra* while still within the maternal uterus, may well be regarded as an adaptation to the needs of embryonic life, but their original development in lung-fishes and Amphibia is evidently a larval feature and was very probably due to the turbidity of the water in which the larvæ lived, which made the ordinary mode of respiration in fishes difficult. On the other hand, there can be no doubt that the transformation of the paired fins of the fish into the terrestrial limbs of the first Amphibia was due to the use of the limbs for supporting the body and moving on land; mere use of the limbs on the ground in shallow water would scarcely have sufficed to bring about so great a structural change, and there is no evidence in the fossil Labyrinthodonts of forms with well-developed terrestrial limbs having gills or gill-clefts in the adult state. We know from the actual structure of the existing lung-fishes that the lungs were

evolved in aquatic vertebrates, *i.e.* fishes, but these fishes still possessed fins, and their descendants only acquired legs when they became terrestrial. Thus Dr. Gadow's conclusion that in the existing perennibranchiate forms the retention of the gills is not an ancestral feature but is due to the persistence of larval organs in adaptation to aquatic habits, is in all probability correct. This is another example of what we may call the zig-zag course of evolution which has taken place in many groups of animals. We shall see that, in fishes, forms most completely adapted to life in the open sea have descended from primitive fringe-finned Ganoids which lived in shallow inland waters, and by the development of lungs had almost become adapted to an air-breathing mode of life; so in Amphibia after the new type had been evolved by a more complete adaptation to terrestrial conditions, not only in the respiratory organs but in the limbs, some of the descendants of this type have returned to the aquatic mode of life and breathe by gills in the adult state. The final results of such a reversal of the course of evolution are however never closely similar to the types from which that course started: the marine bony fishes (Teleosteans) which have a closed air-bladder, or have lost that organ altogether, are not similar in structure to the cartilaginous sharks (Elasmobranchs) from which we have reason to think the bony fishes were originally derived, and the Amphibia which live permanently in water are not fishes although the first Amphibia were evolved from fishes; the direction of evolution may be reversed, but the exact steps are never retraced, and the end of the journey is never the same as the starting-point.

In number of existing species the Amphibia are the poorest of the classes of Vertebrata: the total number is about 1000, of which no less than 900 belong to the Anura or tail-less forms. Of Urodela there are about 100 species and of Apoda about forty. The latter group resemble in their paucity and distribution the lung-fishes among the fishes, and like them have retained more than the other groups some of the primitive characters of the ancestral forms of the Palaeozoic period. In number of species fishes are about eight times as numerous, and reptiles three and a half times, as the Amphibia. Even in the earliest period of their history, the only period for which we have more than the scantiest records, the numbers were not

great in comparison with those of fishes. Very soon after their origin they gave rise to the reptiles which proved themselves more capable of multiplying and possessing the earth. In order to become really abundant any type of animal, whatever the general adaptations or peculiarities of structure which distinguish it, must be able by minor adaptations to accommodate itself to the different conditions of the various regions and localities of the world. The sea, extending over three-fourths of the surface of the globe, affords vast scope for the multiplication of those animals which are able to live in it. Fishes therefore possess an immense space from which the Amphibia are entirely excluded, for these animals in the course of their evolution have never acquired the power of tolerating salt water. By their larval aquatic life the majority of Amphibia are restricted to the neighbourhood of stagnant fresh waters. Reptiles on the other hand, by the development of a firm egg-shell and the embryonic adaptations connected with it, became independent of water and were able to populate the dry places of the earth, while some of them became adapted to arboreal life and some even adopted marine habits. Among the Amphibia only the Anura have shown any great plasticity of organisation, that is to say any capacity for varied adaptations, especially for arboreal life, and this with their great fecundity explains the fact that they are the dominant group among the Amphibia. The class as a whole is to be regarded as merely the survival of the transitional form by which the reptiles were evolved from the fishes, and for this reason is of the greatest interest to the zoologist. There can be little doubt that in many cases such transitional forms have become entirely extinct and not only so but have left scarcely any trace of their existence in the record of the rocks: with the exception of *Archæopteryx*, for example, there are neither survivors nor fossils to show us the intermediate stages between the reptile and the bird.

## CHAPTER III

### DISTRIBUTION AND HABITS

Amphibia usually associated with stagnant fresh water. Geographical distribution. Notogæa and Arctogæa. Oceanic and other islands. Food and feeding. Relations to salt and moisture. Æstivation and hibernation.

AS we have mentioned above, Amphibia live only on land or in fresh water, and usually they are confined to the neighbourhood not merely of fresh water, but to that of stagnant or slowly moving fresh water. This is particularly true of the great majority of species whose eggs are laid or whose larvæ are developed in the water. They live therefore either in or near swamps, marshes, ditches, ponds, sluggish streams or lakes; but there are numerous exceptions which are either viviparous or carry the eggs on their bodies, the young passing through the whole of their development without entering the water. A few species of Anura, e.g. *Chiroleptes platycephalus*, live in the arid regions of Central Australia; they are able to survive by living underground in burrows and by storing up quantities of water in their bodies. Some Anura are almost entirely aquatic in their habits, as *Xenopus* and *Pipa*, others enter the water chiefly in the breeding season, but the most interesting adaptations are those related to arboreal life. Tree-frogs occur in all the forest regions of the world, and are not all of one division of the Order, but occur in all the chief divisions: the Hylidæ among the Arcifera are one of the largest groups of tree-frogs, but among the Ranidæ the Dendrobatinæ in S. America have similar habits, and most of the species of *Hylodes* among the Cystignathidæ are arboreal. *Salamandra atra* is an Alpine species extending to altitudes of 9000 feet in the European Alps; its young are born fully developed but it nevertheless lives in damp and shady places. *Proteus anguinus* and *Typhlonolge rathbuni* are subterranean, the former living in the streams of the limestone caves of Dalmatia, the latter in Texas.

In relation to the geographical distribution of Amphibia the land of the world is divided into two divisions, the first called Notogæa, consisting of Australasia and South America, and the second called Arctogæa, including the rest of the world. The Cystignathidæ among the Arciferous Anura are found only in Notogæa, entirely absent from Arctogæa. In Notogæa Arcifera generally are predominant, forming 90 per cent of the total number of Anura. In Australia Apoda and Urodela are entirely wanting, a curious fact which seems to show that this continent was cut off from the rest of the world until after the evolution of Anura, which were able to extend into it by their greater powers of locomotion. Only one species of the Firmisternia occurs in Australia, namely a species of *Rana* in Cape York peninsula. There is only one Amphibian in New Zealand, namely *Liopelma*, one of the Discoglossidæ.

It is a well-known fact that true oceanic islands, that is, islands surrounded by deep water, such as St. Helena, have no Amphibia; the class is represented in several island groups of the Pacific to the east and north-east of Australia such as the Solomon Islands, but these islands are connected by shoals at no great depth with the Malay Archipelago and so with Asia, and are therefore included in the Palæotropical division of Arctogæa. South America or the Neotropical region, differs from the Australian in the presence of Apoda; Urodela are not entirely wanting, but they are represented only by species of *Spelerves* and *Plethodon*, genera which belong to North America and have evidently extended thence into the southern continent. Besides the Cystignathidæ, Hylidæ, and Bufonidæ, which occur also in Australia, there are Engystomatinæ. A few Raninæ belong to this region, and they probably originally came from the north, but in the forest regions of tropical South America they have been modified into an arboreal sub-family, the Dendrobatinæ, found also in Africa and Madagascar. One of the Aglossa, namely *Pipa*, occurs; Discoglossidæ, Pelobatidæ, and Dyscophinæ are absent.

Arctogæa or the northern world, in which are included India and Africa, differs from Notogæa in the absence of Cystignathidæ. Its main divisions are two, the Periarctic, *i.e.* the great expanse of land round the Arctic circle including Europe, Northern Asia and North America, and the Palæotropical

region consisting of Africa, India and tropical Asia and the Malay Archipelago. The chief characteristic of the Periarctic region is the abundance of Urodela which are almost peculiar to this region and may therefore be considered to have been evolved within it. There are no Apoda. The characteristic Anurous groups are Discoglossidæ, Pelobatidæ, Bufonidæ and Ranidæ. The region can be divided into the Western Palæarctic, eastern Palæarctic or northern Asia, and Nearctic or North America. The eastern Palæarctic shows resemblances to the Nearctic in the presence of Amphiumidæ and Amblystomatinae, while Salamandrinæ are peculiar to Europe. The Palæotropical region is characterised by the absence of Urodela except one species of Amblystoma which occurs in Siam and Burma, while the other species of the genus are American; by the presence of Apoda, and by the great predominance of Firmisternia. Cystignathidæ are absent as from the whole of Notogæa, and of Hylidæ only two occur in the Himalayas which properly may be considered to belong to the Periarctic region. The Amphibian fauna of Madagascar is peculiar in several respects. It differs from both Africa and India in the entire absence of Apoda, of Aglossa and of Bufonidæ. The Malay Islands, Papuasia, and Melanesia agree with India and differ from Africa in the possession of Pelobatidæ, and with southern Asia in the possession of several genera of Raninæ; these islands must therefore with respect to Amphibia be considered to belong to the Palæotropical region and not to the Australian.

All Amphibia in the adult state are carnivorous. The aquatic forms, such as the perennibranchiate Urodela and aquatic Anura, devour Crustacea, small fishes, worms, insects, and in the case of large species such as *Necturus*, frogs. The larvæ, as in the case of the tadpoles of the common frog, on the other hand, are largely herbivorous, but it is a common mistake to suppose that they are entirely so: they eat carrion and, especially in the later stages of development, do not thrive without animal food such as pieces of meat. The terrestrial forms live on worms, insects, snails, and the larger forms will devour other Amphibia smaller than themselves: the American bull-frog preys to a great extent on smaller frogs. The teeth are not of very great importance in

seizing or masticating the food but serve to hold it firmly and prevent its escape from the jaws. The tongue is a great development of muscle in the floor of the mouth attached to the modified branchial skeleton; it makes its first appearance in Amphibia in the vertebrate series and is thus evidently called forth by the requirements of terrestrial existence, that is to say, fishes seizing their food under water, although they can move the ventral parts of the gill-arches in taking food, do not require a specialised muscular tongue and in the most aquatic Amphibia the tongue is rudimentary or wanting. This organ is present in all Amphibia except the Aglossa among the Anura, but is least developed in the aquatic Urodela. It is most developed in the Anura except the Aglossa, which are entirely aquatic, and in which the tongue has been secondarily lost; in the Discoglossidae it shows its most primitive condition adherent by the whole of its base and incapable of protrusion; in the remaining forms it is developed into a long posterior process which is turned forwards and rapidly withdrawn in the capture of prey. It is a common characteristic of Anura that they will not take any food unless they see it move; any one who has reared tadpoles knows that they live and feed well enough until the metamorphosis is completed, but that it is usually impossible to feed and rear the young frogs after they have left the water. The only way to do this successfully is to put small pieces of meat on the end of a wire and make them vibrate in front of the little frogs which will then lick off the morsel with their tongue.

Salt is fatal to Amphibia, the eggs and larvæ are killed by a solution of even 1 per cent. They are therefore unable to live in or to cross seas, salt lakes, or saline plains, although they may occasionally be carried across seas in floating vegetation. Many species are unable to live in waters containing much lime in solution, but others flourish in such waters; the water in which *Proteus* lives, for instance, flowing through limestone caverns, is necessarily saturated with lime salts. Terrestrial Amphibia can tolerate high temperatures with moisture but not cold and drought. As we have seen, Anura abound in the moist forests of the tropics; in the water they are quickly killed by a temperature above  $40^{\circ}$  C. or  $104^{\circ}$  F. but in the air a tree-frog can sit exposed to the sun at a temperature of nearly  $50^{\circ}$  C. or  $122^{\circ}$  F. In this

case, as in a human being, the evaporation from the frog's moist skin keeps its body temperature below a certain limit, but many species with drier skins, such as the toads, habitually avoid the sunshine, and conceal themselves in the daytime in holes or under stones, and many of them in somewhat dry, hot climates aestivate in a torpid condition like the Dipnoi among fishes.

In Central Australia, according to the description of Professor Baldwin Spencer, *Chiroleptes platycephalus* was found in the dry season about a foot from the surface in a "clay-pan," *i.e.* a depression of the ground covered with clay which would be the bottom of a shallow pond in the wet season. The body was distended into a spherical shape and completely filled the cavity which it occupied. This distension was due to the water which the body contained, some in the urinary bladder, some in the subcutaneous spaces, but the greater portion in the body cavity itself.

In temperate climates, on the other hand, Amphibia become torpid in winter, in which condition they cease to breathe air and depend on cutaneous respiration. In this state they can endure any degree of cold provided the internal organs are not completely frozen so that the tissues are killed; the circulation is suspended and the heart ceases to beat, but when the temperature rises again it resumes its functions and the animal becomes as active as before. Frogs and other Amphibia often hibernate in the mud at the bottom of ponds, the pulmonary respiration being suspended when they are in this condition, whereas in summer they would soon be drowned if kept for an indefinite time under water.

## CHAPTER IV

### REPRODUCTION

Tail-less Batrachia, general course of development. Various modes of protecting the eggs: nests in the water and on land. Eggs carried by the parents, round the legs by the male, on the skin or in a dorsal pouch by the female, in enlarged vocal sacs by the male. Pairing in Urodela. Protection of eggs by Urodeles. Salamanders that carry their eggs. Viviparous salamanders.

**I**N frogs and toads, such as occur in temperate climates, pairing and oviposition generally take place in the water, whether the species, outside the breeding season, be terrestrial, burrowing, or aquatic. The male catches hold of the female, either under the arms or round the waist, and awaits, in an embrace that may last days or even weeks, the extrusion of the eggs, which, as he sits on her back, he impregnates by successive emissions of the fertilising elements.

This function over, the pair separate and the eggs are abandoned to their fate, either floating in large masses on the surface, or attached singly or in bunches to submerged objects, or forming strings twined round reeds or other aquatic plants. In most of our northern species, there is a fixed annual period of reproduction, taking place at the end of winter or in spring; but there are exceptions: in the family Discoglossidæ, for instance, members of which breed several times during the spring and summer, at distant intervals; and between these two extreme types, almost every possible gradation intervenes.

Species differ greatly in the choice of a site for depositing their ova, some showing a remarkable discrimination whilst others spawn in ditches or puddles of a most temporary nature (although suitable places may be easily accessible to them) the drying up of which may result in a wholesale destruction of the progeny. But nature has provided for such a waste, the frogs which so behave being at the same time the most prolific.

The eggs of an ordinary frog or toad are spherical bodies, surrounded by a thin membrane and one or two gelatinous envelopes, formed during the passage down the oviducts, the outer capsule swelling out in the water, after oviposition. The upper half of the sphere is more or less pigmented, varying from pale brown to black according to the species, and this coloration may extend to the whole sphere. The eggs are small, usually one or two millimetres in diameter, containing a comparatively small amount of nutritive matter for the embryo, and very numerous, numbering several hundreds or even thousands.

After fecundation the eggs undergo a process of division or segmentation, vertical and horizontal furrows appearing over the whole sphere (extreme holoblastic type), resulting in a great number of cells out of which the tissues of the future embryo are formed. The whole egg becomes converted into the embryo, and this state of things, which, as we shall see further on, is by no means universal in this class of animals, has been one of the great arguments of the celebrated Spallanzani, in the eighteenth century, in favour of the theory of the pre-existence of the embryo in the unfertilised egg. Such a lack of vitelline food necessitates a very early liberation of the larva, in order that it may provide food for itself, and at this period it is of course exposed to much greater dangers than if turned out into the world in a less embryonic condition. The amount of protection which the gelatinous envelopes afford the embryo varies considerably according to the species. In some, these envelopes soon dissolve, so as to release the embryos almost before they are able to execute any spontaneous movements ; they, so to say, drop out and become fixed to the outer surface of the remains of the envelope ; whilst in others they develop much further within the egg and become liberated by their own action.

In the first condition of the larva, the head is large and distinct from the elongate body, the tail absent or rudimentary. The head is cleft below by a longitudinal groove, in the middle of which a transverse or rhomboidal depression represents the first rudiments of the mouth ; on each side and in front of this depression, a pit indicates the nostril, and behind it is a grooved, curved or angular transverse fold which

develops into a single or paired prominence, the "holder," often improperly called "sucker," acting as an adhesive apparatus by means of which the helpless larva fixes itself at first to the outer surface of the mucilaginous envelope of the egg, and later to weeds or submerged objects. Eyes are absent. A small bud-like tubercle on each side of the posterior border of the head is the rudiment of the external gills, and vertical folds in front of and behind the bud represent the visceral clefts, the

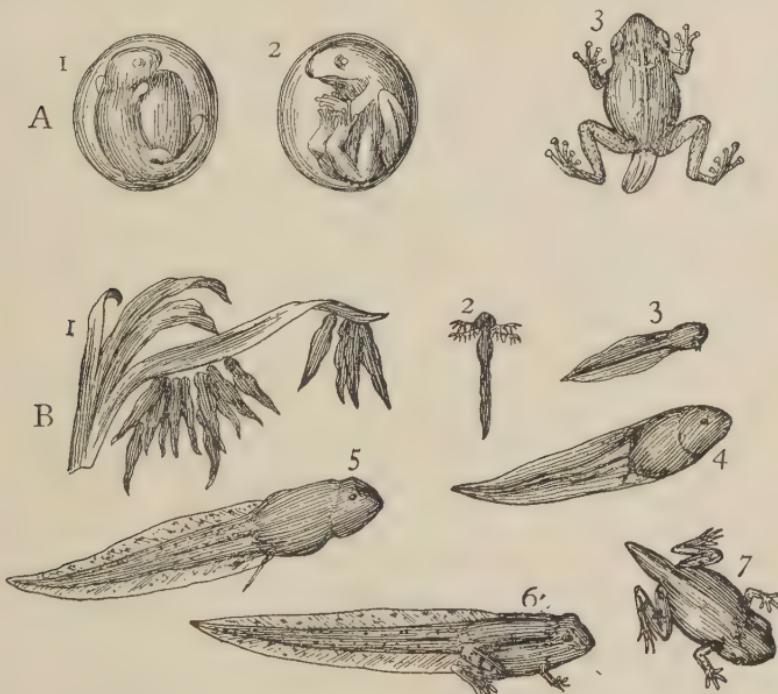


FIG. 13.—A, Development of *Hyloides martinicensis*. 1, embryo seven or eight days old; 2, twelve days old; 3, young just hatched. B, Stages in metamorphosis, of Common Frog. 1, tadpoles soon after hatching; 2, tadpole with external gills, from above; 7, young frog.

intervals between which will later become converted into the four branchial arches.

As the larva grows, the tail lengthens and shows a muscular portion with chevron-shaped divisions (myotomes), bordered above and below by a vertical membrane. The external gills appear as digitate or branched appendages; the olfactory pits shift more forwards, and become converted into functional nostrils communicating with the mouth; the eye may be detected at the side of the head, appearing first as a pig-

mented ring under the transparent epidermis ; the mouth becomes bordered by fleshy lips ; the anus is perforated ; and the larva (we shall not yet call it a tadpole) is able to feed, having thus far subsisted on the yolk contained in the abdomen. (Fig. 13, B, 1, 2.)

On entering the second period, or true tadpole stage, an opercular fold covers the external gills, which atrophy and are replaced by internal ones—small branched filaments disposed along cartilaginous arches. An anal tube is developed ; the mouth acquires horny, beak-like mandibles, and the funnel-shaped lips horny teeth ; the nostrils assume a more dorsal position ; the "holder" disappears ; and the opercular fold having fused with the skin above the gill-arches, leaving an opening (spiraculum) for the egress of the water from the gill-chamber, the head becomes confluent with the globular, swollen body, in which the extremely elongate gut shows through the transparent abdominal membrane, coiled up like a watch-spring. (Fig. 13, B, 4, 5, 6.)

In the third period, the hind limbs appear as buds at the base of the tail, and gradually attain their full development during the tadpole life. (Fig. 13, B, 5.) The fore limbs grow simultaneously, and even more rapidly, but remain concealed within a diverticulum of the branchial chambers until fully formed, when they burst through the skin (unless the left spiraculum be utilised for the egress of the corresponding limb). (Fig. 13, B, 6.) Then only the caudal fin-membrane becomes reduced and the tail is gradually absorbed ; the gills entirely disappear ; the lungs, which had co-existed as accessory respiratory and hydrostatic organs, assume alone (or, rather, together with the skin) the respiratory function ; the horny armature of the mouth and lips is shed in pieces ; the lips are absorbed and the buccal cleft extends ; the eyes become free and acquire movable lids ; the intestine shortens ; and the young frog, usually still bearing a stumpy tail, leaves the water. (Fig. 13, B, 7.) The metamorphosis is completed.

Such is, briefly sketched, the development of the typical frog or toad. But there are many exceptions to this course, especially among species living between the tropics ; and we shall now deal with some of the more interesting examples with which we are at present acquainted.

Eggs deposited simply in the water and larvae which pass through a lengthy metamorphosis in that element are naturally exposed to many dangers, hence the enormous number, often amounting to thousands, produced by one female annually. On the other hand, many contrivances have been resorted to by which the young are protected during their frail, early stages, in which case Nature has practised economy in the number of eggs, which varies in direct proportion to the chances of destruction.

These contrivances fall under two heads, which may be found combined in some forms: firstly, protection by the parents, either by means of nests or nurseries, or by direct nursing; secondly, shortening of the metamorphosis, which is hurried through within the egg, the young leaping out into the world in the perfect condition in which ordinary frogs leave the water. The different modes of protection will be made clear by the following synoptic arrangement:—

- (1) Protection by means of nests or nurseries.
  - A. In enclosures in the water.
  - B. In holes near the water.
  - C. In nests, on trees or rocks, overhanging the water.
  - D. In a transparent gelatinous bag in the water.
  - E. On trees or in moss away from the water.
- (2) Direct nursing by the parents.
  - A. Tadpoles transported from one place to the other by the male.
  - B. Eggs protected by the male, who covers them with his body.
  - C. Eggs carried by the parent.
    - a.* Round the legs by the male.
    - b.* On the back of the female.
      - a.* Exposed.
      - β.* In cell-like pouches.
      - γ.* In a common pouch.
    - c.* On the belly, exposed, by the female.
    - d.* In the mouth, or in a gular pouch.
      - a.* By the male.
      - β.* By the female.
  - D. Eggs retained in the uterus (viviparous species).

The examples given hereafter will be dealt with in the same order, and under the same lettering.

(1) A. A large tree-frog (*Hyla faber*) known in Brazil as the "Ferreiro" (=smith) from its peculiar voice, sounding like a mallet slowly and regularly beating upon a metal plate, protects its progeny by building basin-shaped nurseries in the shallow water of the borders of ponds. The mud is scooped out by the female to a depth of three or four inches, and with the material thus removed a circular wall or parapet is built which emerges above the surface of the water. The frog uses its webbed, flattened hands for smoothing the inside of the mud wall, as would a mason with his trowel, whilst the levelling of the bottom of the basin is performed by the action of both belly and hands. These nurseries, the aspect of which may be compared to the crater of an extinct volcano, measure nearly a foot in diameter. The eggs and early larvæ, which do not depart from the normal type described above, are thus protected from the attacks of many aquatic insects, fishes, or other batrachian larvæ, at least for a time, for it is not unusual for heavy rains to destroy the walls of the enclosure and thus to prematurely release the larvæ.

(1) B. A still better mode of protecting the offspring during the early stages of development has been adopted by a Japanese tree-frog of the family Ranidæ (*Rhacophorus schlegelii*). The male and female in embrace bury themselves in the damp earth on the edge of a ditch or flooded rice-field, and make a hole or chamber, a few inches above water-level; after polishing the walls of this chamber, during which process the gallery by which they gained access to it becomes completely obliterated, oviposition begins. The female first produces from the vent a secretion which, by rapid movements of the feet, is beaten up into froth and afterwards, in the midst of this agglomeration of air-bubbles, she deposits the eggs; the male, who has all along been clinging to her back without taking part in the operation, at once impregnates them. This being accomplished, the pair separate and proceed to make their way out of the chamber by boring a gallery of exit; instead of returning the way they came, the tunnel which they now bore is in the side of the bank and directed obliquely downwards towards the water; and this tunnel will be utilised later by the larvæ to gain access

to the ditch or pond, in which they will complete their metamorphosis. The eggs are well protected and aerated by the mass of air-bubbles in the frothy mass surrounding them, which lasts until, after a few days, the larvæ are able to move, when, by the collapse of the bubbles and the liquefaction of the froth, a most efficient vehicle is afforded by which the tiny larvæ are carried down the tunnel into the water.

The eggs of this *Rhacophorus* are about one millimetre in diameter and absolutely devoid of pigment; the segmentation, though holoblastic, is of a type approaching the meroblastic, as in other Batrachian eggs containing much yolk; the embryo is at first quite distinct from the yolk. Eggs taken from the nest invariably die if put into water. The tadpoles, when leaving the nest, are said to resemble those of ordinary frogs.

Some species of the South American Cystignathid genera *Leptodactylus* and *Paludicola* have been observed to treat their eggs in a somewhat similar manner. In the breeding season the parents prepare a hole under a stone or decayed wood, near the edge of a pool, above the water-line. The eggs, in small number and of light colour, are also surrounded by a frothy substance, in which the larvæ attain a certain development, until, after rain, the pool overflows and they are washed into it.

The little Australian Bufonid, *Pseudophryne*, deposits its large eggs under stones or on the edge of a dried-up pool. The larvæ do not emerge until rain has again filled the pool.

(1) C. Some tree-frogs, *Phyllomedusa* in South America, *Rhacophorus malabaricus* in India, and *Chiromantis* in tropical Africa, deposit their spawn on trees, in nests of froth attached to a leaf or to several leaves stuck together, and overhanging a pool. The larvæ move with considerable freedom in the frothy mass, and after a few days, having lost the external gills, drop into the water, where they complete their metamorphosis in the ordinary way. As in the preceding forms, the eggs contain much yolk, and are comparatively few in number, viz. not over 200.

Nests very similar to the above have been observed in Japan, and ascribed to *Rhacophorus schlegelii*, but this determination requires confirmation. Other species of *Rhacophorus* inhabiting India and Ceylon, produce masses of green frothy spawn which have been found sticking to the walls of wells, per-

pendicular rocks in quarries, or trunks of trees, in such a position as to allow the larvæ to readily drop into the water when strong enough to swim about and procure their food, this being but a simplified *variante* of the nests which some of their congenera are known to produce.

(1) D. Another form of nest is that offered by a small Engystomatid from New Guinea: *Phrynxalus biroi*. The large, impregnated eggs, measuring seven millimetres in diameter, and only twelve to eighteen in number, are enclosed in a sausage-shaped transparent common membrane, secreted by the female, which is abandoned in mountain streams. As in *Hylodes*, the whole development takes place within the egg, which the little frog leaves in the perfect condition. No gills have been observed and the large tail serves as a breathing organ whilst the young is in the egg.

(1) E. In several species of the tropical American genus *Hylodes*, small tree-frogs related to *Leptodactylus*, of which the West Indian "Cogni," *H. martinicensis*, is the best known, the eggs are deposited in damp places, under stones or moss or on the leaves of plants, and are of large size. The metamorphosis is hurried through within the egg, and after subsisting on the large yolk-bag, the young frog hops out as an air-breather, with a mere vestige of the tail which was fully developed and so richly supplied with blood that it no doubt functioned as a breathing organ, no gills or gill-slits having been detected. (Fig. 13, A.)

Another small tree-frog of the family Hylidæ, *Hylella platycephala*, from Mexico, is said to lay its eggs in the axils of the leaves of *Tillandsia*, where it undergoes the whole of its metamorphosis.

A large frog inhabiting the Solomon Islands, *Rana opisthodon*, morphologically very similar to our European species of the same genus, also undergoes the whole of its development in the egg and away from water. The eggs, which measure six to ten millimetres in diameter, have been found in the moist crevices of rocks, with the small frog coiled up, in an advanced state of development, without even a vestige of a tail and differing from the perfect frog only in the presence of several folds of skin on the sides of the belly, the function of which is probably that of breathing organs, like the tail of

*Hylodes*, and of a small, hard, conical protuberance at the end of the snout, which, like the well-known egg-tooth of many higher vertebrates, is used to perforate the rather tough envelope of the egg.

A curious frog from the Malay Peninsula, *Megalophrys longipes*, of the family Pelobatidæ, measuring only sixty millimetres from snout to vent, is believed to deposit its ova in clusters of about a dozen under damp moss or tree trunks, the young emerging in the perfect condition. These eggs are most remarkable as being the largest on record among frogs, their diameter being thirteen millimetres.

(2) A. Small South American frogs of the genera *Dendrobates* and *Phyllobates*, not very far remote from the typical Ranids, have been repeatedly observed carrying well-developed tadpoles on their back. These tadpoles are essentially similar in form and anatomical structure to those of our European frogs, and they adhere to the back of their parent by their sucker-like lips and flattened abdomen. It has been observed in the case of *Dendrobates trivittatus* that the frog spawns in water, and that the free-swimming tadpoles attach themselves to the parent—which, in *Phyllobates trinitatis*, has been ascertained to be the male. It is inferred that the young are thus transported from one pool to another, an excellent plan to adopt in districts where the water may dry off in two or three days.

The frog in which this mode of nursing had been first observed in the Guianas had been determined as *Hylodes lineatus*, but the figure which accompanies its description shows it to have been probably a *Phyllobates* or *Dendrobates*. The true *Hylodes lineatus* has since been observed, in Peru, to lay its eggs under grass far from water, and the young before hatching are perfect little frogs, without even the remains of a tail.

A somewhat similar little frog in the Seychelles, *Sogglossus sechellensis*, also carries its tadpoles. It is found in forests at about 5000 feet altitude, where there is no still water. The eggs are concealed under dead leaves, and the tadpoles, as soon as hatched, place themselves, with the aid of their tails, on the male's back, to which they stick partly by suction, partly by a viscous secretion produced by the parent. The tadpoles are not attached to the parent for transportation

to water, but undergo in that position the greater part of their development; no gills have been found in them, only the usual rudiments of lungs.

(2) B. The eggs of a Papuan frog allied to the *Phrynxalus* mentioned above ((1) D.), *Mantophryne robusta*, are strung together by an elastic gelatinous envelope similar to that known in the European Midwife Toad, and, seventeen in number, form a clump over which the male sits, holding it with both hands. The diameter of these eggs is six or seven millimetres, and on the occasion on which they were observed each contained an embryo with well-developed legs, no gills, and a large tail, the membranous lobes of which are rich with capillary vessels and



FIG. 14.—Midwife Toad (*Alytes obstetricans*): a, male with eggs; b, female.

act no doubt as a breathing organ. Here again, as in *Phrynxalus*, the mode of development is essentially the same as in *Hylodes*; like the latter, and unlike the former, it takes place out of the water.

(2) C. a. We now come to the well-known example of the Midwife Toad, *Alytes obstetricans*, discovered in France in the middle of the eighteenth century, in the very act which has rendered it famous. (Fig. 14.) For over a century it, with the equally famous Surinam Toad, remained the only known examples of parental solicitude among the batrachians.

Pairing and oviposition take place on land. The male first seizes the female round the waist, and when, after having submitted to a process of lubrication of the cloacal region by rapid

movements of his toes, she stretches out her hind limbs, he places his between them, bent at angles at the knees, the tarsi erect and pressed close together, thus forming a receptacle in which the eggs are suddenly extruded. The yellow eggs, as if threaded together by elastic filaments continuous with the gelatinous capsules, form a large mass, two to four layers of about ten eggs, in this receptacle. The very moment the eggs are produced, the male unclasps the waist of the female and shifts his hold to the base of the head ; the body then stretched out, but the legs remaining in the same position as before, fecundation commences ; it takes place in two or three emissions at short intervals. After a few minutes' rest, the male proceeds to attach the strings of eggs to his legs, by passing the latter into the egg-mass and then folding them against his body. There they remain until hatched. Thus laden, and yet so little impaired in his movements as to occasionally resort again to hymen during the nursing period, and successfully add on a second burden, the male retires to his usual retreat, in a hole in the ground, or between the stones of some old wall, but going about at night in order to feed himself and to keep up the moisture of the eggs, even resorting to a short immersion in the water during exceptionally dry nights. The development in the egg takes about three weeks. At the expiration of this period, he enters the water with his burden ; the larvæ, in the full tadpole condition, and limbless, measuring fourteen to seventeen millimetres, bite their way through the tough envelope or egg-string, which is not abandoned by the father until all the young are liberated. The rest of the development does not differ from that of other frogs.

The rosary-like string contains about twenty to fifty eggs, which, considering the small size of the frog (forty to fifty millimetres from snout to vent) are remarkably large, measuring three and a half to five millimetres in diameter. When first laid the eggs are nearly spherical, but they soon acquire a more oval shape. Through the transparent capsules the whole development can be easily followed. An enormously large vitelline sac is present, and the embryo is provided with uncommonly long, unpigmented, branched external gills, one only on each side, which are absorbed and replaced by internal ones before the larvæ are hatched.

(2) C. b. a. In a Brazilian tree-frog, *Hyla goeldii*, it is the female which takes charge of the eggs, carrying them on the back. How they get there is still unknown, but we may surmise that they are placed by the male. The whole surface of the back is occupied by one layer of twenty-six large yellow eggs, four millimetres in diameter, on which, in the specimen described, the embryos, coiled round the enormous vitelline sphere, can be distinguished with the naked eye. The skin of the back is extended into a narrow fold which borders and supports the egg-mass on the sides, thus suggesting an incipient stage of the dorsal pouch to be described hereafter in the allied genus *Nototrema*. (Fig. 15.) The embryos

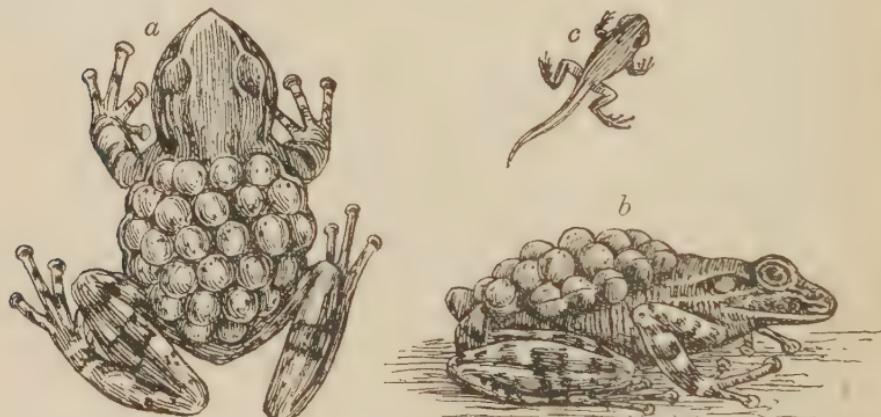


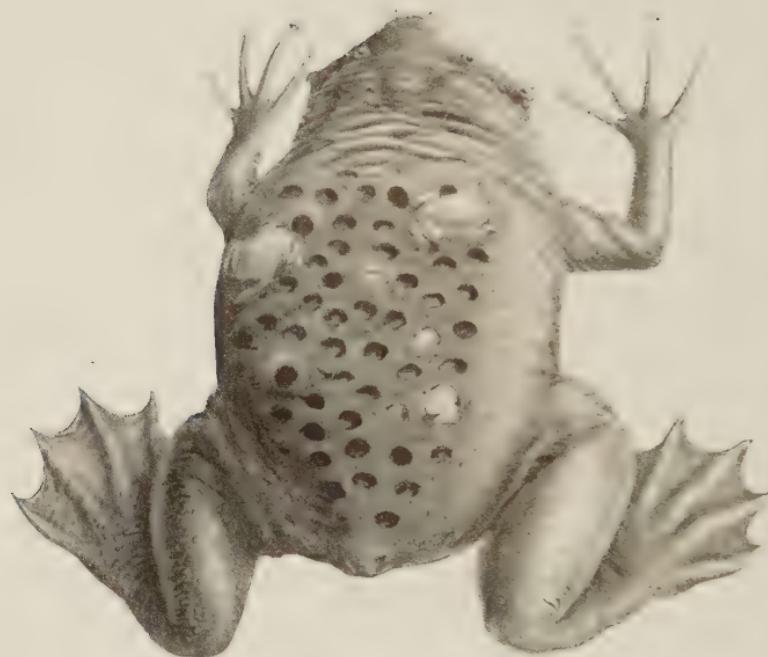
FIG. 15.—*Hyla goeldii*, a tree-frog carrying eggs on its back: a, from above; b, from the side; c, young when hatched.

are much elongate in shape, colourless, with a large flat head, in which the eyes are distinguishable as two black points; no traces of gills are to be seen. The young leaves the egg in the perfect state, but still provided with a longish tail.

An allied, but larger, species from British Guiana, *Hyla evansii*, has adopted the same mode of nursing. The eggs, twenty-two in number, measure eight or nine millimetres in diameter.

A frog of the family Hemiphractidæ, *Ceratohyla bubalus*, an inhabitant of the Andes of Ecuador, Bolivia, and Peru, also carries its eggs on the back. A female specimen, measuring sixty-three millimetres from snout to vent, has been obtained in Peru, carrying nine large spherical eggs, ten millimetres in diameter, each containing a little frog distinctly visible





SURINAM TOAD (*PIPA AMERICANA*). FEMALE. WITH YOUNG ESCAPING FROM CELLS IN SKIN OF BACK



*NOTOREMA MARSUPIATUM* WITH DORSAL POUCH HALF DEVELOPED

SAME WITH POUCH FULL OF EGGS

(AFTER GÜNTHER)

through the transparent membrane which at this stage constitutes the egg-capsule. The little one, with the abdomen, tumid with yolk, turned towards the back of the mother, and the limbs folded against the belly, is connected with the membrane by two string-like cords on each side, proceeding from the throat, such as we shall describe presently in some species of *Nototrema*, and these cords serve to convey the blood, for the purpose of respiration, to the vascular, allantois-like membrane.

(2) C. b.  $\beta$ . In the preceding examples, the eggs are simply adherent to the back, leaving shallow hexagonal impressions in the skin. In the well-known Surinam toad, *Pipa americana*, an inhabitant of the Guianas and Northern Brazil, the eggs are likewise carried on the back of the mother, but the skin thickens and grows round the eggs, until each is enclosed in a dermal cell, which is finally covered by a lid, believed to be formed by a secretion from the glands of the skin. (Plate XVI., A.) The eggs, which may number about 100, and measure five to seven millimetres in diameter, develop entirely within these pouches, and the young leap out in the perfect condition, without even a vestige of a tail. External gills exist but are lost at a very early period, and a long tail is present in the embryo.

The *Pipa* is a thoroughly aquatic Batrachian, and pairing of course takes place in the water. The male clasps the female round the waist. The way in which the eggs reach the back of the female has been observed in specimens kept in the London Zoological Gardens. During oviposition the cloaca projects from the vent as a bladder-like pouch, which is directed forwards, between the back of the female and the breast of the male, and by means of this ovipositor the eggs are evenly distributed over the whole back. How the eggs are fertilized has not been ascertained.

(2) C. b.  $\gamma$ . Whilst in the *Pipa* each egg is enclosed in an outgrowth of the skin of the female's back, in the South American tree-frogs of the genus *Nototrema* the whole of the brood is sheltered in a common pouch, a structure which, as we have seen, is foreshadowed by the lateral everted fold of *Hyla goeldii*. This dorsal pouch develops only at the approach of the breeding season, and is evolved by the skin of

the back forming a horse-shoe-shaped fold on the sacral region, which gradually deepens; the inner wall of the pouch is therefore part of the outer layer of the skin turned inwards. (Plate XVI., B, C.) How the eggs are introduced into the pouch is still unknown. In most species of this genus, the opening to this invaginated dorsal fold is small and situated on the posterior part of the back, often so small, when the pouch is distended by the ova, as to simulate a second anal opening. In one species, however, *Nototrema pygmæum*, from Venezuela, the pouch is formed by two lateral folds, meeting on the middle line of the back, a mere slit separating them when the back is filled with eggs.

In some species, *Nototrema marsupiatum*, and *N. plumbeum*, the eggs are large and numerous (about 100), and, as in *Alytes*, only a part of the metamorphosis is undergone within them, the young escaping from the pouch as ordinary tadpoles, with a powerful tail, internal gills, and a beak-like mouth surrounded by a large circular lip. In others, *N. oviferum*, *N. testudineum*, *N. fissipes*, *N. cornutum*, and *N. pygmæum*, the eggs are enormous and few in number (four to sixteen) and in these species the whole development takes place within the pouch, which the young frog leaves in the perfect condition, differing only in size from its parents. Within the pouch, the breathing organs of the larvæ consist of a pair of bell-shaped membranes, veined with a capillary network, each connected with the second and third branchial arches by a pair of string-like filaments. These gills, the form of which can only be seen by floating them in water, form a sort of envelope to the embryo, like an allantois, and may be designated by the term allantoic gills, which has been proposed for the lobate gills of the Tailed Batrachian *Autodax*.

*Amphignathodon guentheri*, the sole representative of the family Amphignathodontidæ, which inhabits the Andes of Ecuador, is provided with a dorsal pouch similar to that of *Nototrema marsupiatum*, but the eggs are still unknown.

(2) C. c. The female of the Ceylonese *Rhacophorus reticulatus* carries its eggs on the belly, which bears shallow impression when the eggs are removed. These, in the single specimen observed, measuring forty-seven millimetres from snout to vent, were spherical and unpigmented, four to five millimetres in

diameter and about twenty in number. Nothing further is known of the breeding habits and development.

(2) *C. d. a.* One of the most remarkable modes of nursing is that of the Chilian *Rhinoderma darwini*, a small frog of the family Engystomatidae. It was first believed to be viviparous, but a more careful examination revealed the fact that the young, about ten to fifteen in number, are sheltered and develop in



FIG. 16.—A, *Rhinoderma darwini* external appearance. B, A specimen of the same with the gular sac cut open, showing contained embryos.

the gular pouch (the modified vocal sac with which the males of many Tailless Batrachians are provided) of the father, which pouch extends over the entire ventral side. (Fig. 16.) No gills or other breathing organs have been observed, and the tail, which is never large, is absorbed before the young leaves the paternal pouch. We do not know how the young get into the pouch, but it is highly probable that the male takes the eggs into his mouth as soon as they are deposited and, with

the aid of his hands, forces them into the subgular vocal sac which, as usual, communicates with the floor of the mouth by a long slit on each side of the tongue.

(2) C. d.  $\beta$ . The female of a West African tree-frog, *Hylambates breviceps*, carries the eggs in her mouth, as do some Silurid and Cichlid fishes. These eggs are large (four millimetres in diameter) and few in number.

(2) D. Two small East African toads, one referred by Tornier to *Pseudophryne* (*P. vivipara*), the other by me to *Nectophryne* (*N. tornieri*) are known to be viviparous, but no observations have yet been made on them beyond the fact that larvæ are found in the uteri.

## II. Tailed Batrachians.

Whilst in all Tailless Batrachians, with the exception of the two viviparous toads, fecundation takes place after the extrusion of the eggs, as in most fishes, in the Tailed Batrachians (salamanders, newts, etc.) impregnation is as a rule internal. There is, however, no copulation in the strict sense, as we shall find in the following order, the Apodal Batrachians, but the spermatozoa are absorbed by the female. The male, after lengthy and varied amorous preludes or evolutions around the female, or after a period of embrace, emits, at short intervals, several conical or bell-shaped spermatophores, adhering to the ground or to stones by their base and crowned by a bunch of spermatozoa which the female gathers with the lips of her cloaca, either by mere application or by her holding the spermatophore between her hind legs and pressing the mass of spermatozoa into the cloaca. In *Cryptobranchus* (and probably also in *Megalobatrachus*) the fecundation is believed to be external.

In most newts (*Molge* or *Triton*), our British species in particular, and in the axolotl (*Amblystoma*), with which we are familiar as an aquarium animal, the courtship is not accompanied by any sort of enlacement; all the male does is to execute the most lively antics in front of the female, and to occasionally hit her with his snout or rub himself against her to entice her to respond to his advances—a sight witnessed by all who have kept our smaller newts in an aquarium in the early spring, the larger British species (*Molge cristata*), for some

unexplained reason, very seldom engaging in courtship when in captivity. But a certain number of Tailed Batrachians are known to spend a longer or shorter part of the breeding season in sexual embrace; for instance the land salamanders (*Salamandra*), some American newts (*Molge viridescens*, *M. torosa*), the Pleurodele newts of Spain and Algeria (*Molge waltlii*, *M. poireti*), and the so-called *Euprocti* of the mountains of Southern Europe (*Molge aspera*, *M. montana*, *M. rusconii*). The mode of amplexus varies.

In the following synopsis, the forms of which the mode of reproduction is known are arranged according to their mode of pairing.

1. No amplexus, but a lengthy courtship in the water; male more brilliantly coloured than the female, and ornamented with dorsal and caudal crests or other temporary dermal appendages.—The true newts (*Molge cristata*, *M. vulgaris*, etc.).
2. Amplexus takes place; no marked sexual differences of colour; no dermal ornamental appendages.
  - A. Amplexus of short duration and partly or entirely on land.—*Salamandra*, *Salamandrina*, and probably all other viviparous or terrestrial species, such as *Spelerpes fuscus*, *Chioglossa*, *Plethodon*, and *Autodax*.
  - B. Amplexus of more or less lengthy duration and in the water.
    - a. The male, distinguished by a greater development of the fore limbs, clasps the female in the axillary region with the fore limbs.—*Molge (Pleurodeles) waltlii*, *M. poireti*, *M. torosa*.
    - b. The male, distinguished by a greater development of the hind limbs, and often by a prehensile tail, clasps the female in the lumbar and caudal regions.—*Molge viridescens*, *M. (Euproctus) rusconii*, *montana*, *aspera*.

This coincidence of courtship and sexual ornaments in the male is highly suggestive of sexual selection. For in the forms

in which, as in frogs and toads, the male takes forcible possession of the female—she being secured by the first comer, without much chance of his being dislodged by any rival, so tight is his hold, no ornaments ever exist. Although in Tailless Batrachians, in which amplexus is universal, there are many secondary sexual differences, these are never capable of being interpreted as in the nature of ornaments.

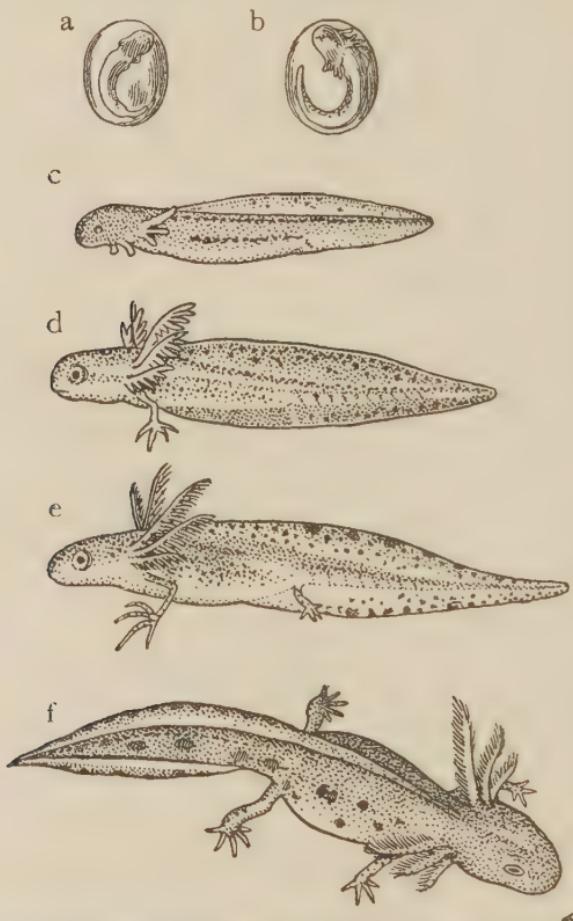


FIG. 17.—Development of Crested Newt : a, b, stages within the egg ; c, d, e, f, stages of the larva magnified.

The different types of eggs vary to the same extent as in the Tailless Batrachians, but they are never so completely abandoned as is the case in many frogs. In the forms which take the least care of their progeny, as in newts and the axolotl, the eggs are deposited, one by one or in small groups, attached to stones or water weeds, the female often

folding a leaf with her hind limbs, so as to afford some protection to the egg. The eggs of these Batrachians are quite small and soon become converted into the whole embryo. The development is not very unlike that of ordinary frogs, but the tadpole stage, characterised by a swollen body, a mouth armed with a horny beak and surrounded with lips beset with horny teeth, internal gills enclosed in a diverticulum of the skin, in which the fore limbs grow without being visible externally, does not exist. The body in most larval forms does not differ much from that of the adult, three pairs of branched, fringed, or tufted external gills are present, the jaws and the palate are beset with teeth, differing in their disposition from the final dentition, and the fore limbs grow before the hind pair. (Fig. 17.)

But other forms afford better protection to their offspring, which are not abandoned to themselves until they have reached a much more advanced condition, either by being retained in the body of the mother, or by being provided with a much greater amount of food-supply within the egg, which again may be guarded by one of the parents or sheltered in a nest. These interesting cases, most of which have only come to light within the last few years, are here arranged in a similar order to that adopted when dealing with the Tailless Batrachians.

- (1) Protection by means of nests or nurseries.
  - A. In holes on land or in trees.
  - B. In a transparent bag in the water.
- (2) Direct nursing by the parent.
  - A. The mother coils herself round the eggs.
  - B. The father coils himself round the eggs.
  - C. The mother carries the eggs on her back or round the body.
  - D. Eggs retained in the oviducts (viviparity).
- (1) A. The species of *Autodax*, a genus of Californian salamanders of terrestrial and nocturnal habits, lay their twelve to twenty eggs in a dry hole in the ground or, more frequently, in a hole in a tree, up to thirty feet above the ground. The mother, or both parents, remain in the hole during the development, the object being probably to maintain the eggs in the high degree of moisture essential to their development, and

also to defend the brood. *Autodax* derives its name from its formidable teeth, and it has been observed to use them when disturbed, snatching fiercely at intruders. The spherical eggs measure about six millimetres in diameter and are firmly anchored to the earth or bottom of the hole by a narrow peduncle about eight millimetres long, of the same substance as the gelatinous capsule surrounding them, these peduncles converging towards the basal point of attachment of the bundle. The embryo is quite distinct, at first, from the large yolk sphere; it has large lobate gills (allantoic gills) quite different from the fringed gills of newts and salamanders. When the young emerges from the egg-capsule, the gills at once wither away and the little *Autodax* enters the world in the perfect condition, measuring thirty-two millimetres in length. The young are believed sometimes to remain for a long time in the hole with their parents.

(1) B. *Salamandrella keyserlingii*, a very small aquatic salamander from Siberia, deposits its eggs in a gelatinous bag, fifteen centimetres long, attached at one end to aquatic plants, just below the surface of the water. This bag is more or less sausage-shaped and contains fifty to sixty small eggs; the larvæ when hatched drop to the bottom of the bag and are liberated in a moderately advanced state of development, measuring ten millimetres, and provided with large external gills but limbless.

(2) A. *Plethodon*, a genus of small terrestrial salamanders inhabiting North America, rears its brood on land. In *P. cinereus*, the eggs are laid in small packages of about five, beneath stones, and the mother remains coiled around them. The larva subsists on a large spherical yolk and does not leave the gelatinous capsule of the egg until after the loss of the gills, which are long and branched, and three in number. *P. oregonensis* has similar habits. A female was found under a decaying log in a wood in California, tending three eggs, similar in size and form to those of *Autodax*. They were covered with a thin gelatinous coating, causing them to stick together. When placed in a jar, the salamander again took charge of the eggs, lying beside them and holding them in a loop of her prehensile tail. Dissatisfied with their position and surroundings, she moved the eggs from place to place in the jar, always holding

them in the crook of the tail. The development could not be followed.

(2) B. The gigantic salamander of China and Japan (*Megalobatrachus maximus*) and its smaller North American ally (*Cryptobranchus alleganiensis*) are thoroughly aquatic, never leaving the water. The egg is a spherical or oval mass of yellow yolk, about six millimetres in diameter in either species; it is surrounded by two or three layers of transparent jelly, forming a large capsule, thirteen to sixteen millimetres in diameter. Unlike the eggs of most Batrachians in which the yolk-sac is large, the egg is far from filling its capsule, but is surrounded by an aqueous fluid. Each capsule is connected with the next by means of a comparatively small string of the same substance, which is at least equal in length to the longer axis of the capsule. The eggs of *M. maximus* have been found in Japan, deposited in deep holes in the water, where they form large clumps (seventy to eighty eggs) round which the male coils himself. The gigantic salamander has also bred in the Amsterdam Zoological Gardens, the eggs numbering upwards of 500. In this case it is the male who is believed to have taken charge of the eggs, and for the ten weeks which elapsed until the release of the last larva, he kept close to them, at times crawling among the coiled mass of egg-strings or lifting them up, evidently for the purpose of aeration. The larva on leaving the egg is about an inch long, provided with three branched external gills on each side, like those of our newt larva, or of the axolotl, and showing mere rudiments of the four limbs.

*Amphiuma*, a member of the same family as *Megalobatrachus* and *Cryptobranchus*, and a native of the South-Eastern United States, has quite similar eggs, the capsule measuring eight to twelve millimetres in diameter. The eggs have been found in a hole in a dried-up swamp, with the mother coiled round them. The larvae on the point of hatching, have four limbs and three long pinnate external gills.

(2) C. *Desmognathus fusca*, a small salamander living in running brooks in the Eastern United States, lays its eggs likewise in rosary-like strings. The female takes charge of this rosary by winding it several times round the body and nurses it in a comparatively dry spot. Sometimes the eggs form a bunch, which is carried on the back of the parent. The spheri-

cal eggs, twenty or more in number, measure four or five millimetres in diameter; they are unpigmented and were first believed to be of the meroblastic type. A more careful investigation has, however, shown that the cleavage extends through the whole ovum. The segmentation is holoblastic, but of that same intermediate type which has been observed in *Alytes*, *Rhacophorus*, and other forms in which the growing embryo occupies a position on the yolk strikingly like that of a fish embryo. The total cleavage is slow in appearing, and in the later stages of development the yolk-mass becomes homogenous by the disappearance of cell-walls. The larvæ, breathing through external gills, remains in the egg-capsule until about twenty to thirty millimetres in length, the rest of the development being undergone in the water. Except for the fact that the female instead of the male takes charge of the progeny, the development of *Desmognathus* is a very close parallel to that of *Alytes*.

(2) D. The genus *Salamandra* is represented in Europe by two very closely allied species, of terrestrial habits, which are both viviparous; but whereas in one the young are born as a rule in the branchiate, larval condition, the other gives birth to perfect salamanders, differing only in size from the parents, and fitted for terrestrial life.

The first species, the yellow-spotted or fire salamander, *S. maculosa*, lives in the plains or at low altitudes in the mountains (up to 2800 feet). It pairs on land, and several months later the female goes to the water and gives birth to ten to fifty young, of small size and similar to newt larvæ with the four limbs developed.

The second species, the black salamander, *S. atra*, is of smaller size and inhabits the Alps between 2000 and 9000 feet altitude. Localities at such elevations are not, as a rule, suitable for larval life in the water, and the young are therefore retained in the uterus until the completion of the metamorphosis. Only two young, rarely three or four, are born, and these may measure as much as fifty millimetres at birth, the mother measuring only 120. The mode of reproduction of this salamander is very remarkable indeed, and unique of its kind. The uterine eggs are large and numerous, but as a rule only one fully develops in each uterus, the embryo being nourished on the yolk of the other eggs. The embryo passes

through three stages: 1, still enclosed within the egg and living on its own yolk; 2, free within the vitelline mass, which is the product of the other, degenerate eggs and which is directly swallowed by the mouth; 3, there is no more vitelline mass, but the embryo is possessed of long external gills, which serve for an absorption of nutritive fluid from the maternal uterus, these gills functioning in the same way as the chorionic villi of the mammalian egg. Embryos in the second stage, if artificially released from the uterus, are able to live in water, in the same way as similarly developed larva of *S. maculosa*. But the uterine gills soon wither and are shed, and are replaced by other gills differing in no respect from those of its congener. And it has recently been ascertained that females of *S. atra* from the lower limit of the vertical range of the species occasionally produce their young as larvae and in increased number (three or four instead of two), whilst, on the other hand, at high altitudes *S. maculosa* may produce young in the perfect condition and few in number.

There is strong reason to suppose that *S. atra* is directly derived from its very close ally *S. maculosa*; and in this connection it is interesting to observe the complete passage which exists between the two species as regards their mode of gestation, the extremes of which are so very different.

*Spelerpes fuscus*, a small Italian salamander, which climbs like a tree-frog, is usually found in limestone caves in which there is no water. It has been ascertained on specimens kept in confinement that the young are born, four in number, in the perfect condition. The development has not been observed, but it is probably similar to that of *Salamandra atra*.

*Proteus anguinus*, the blind perennibranchiate Urodele of the caves on the East coast of the Adriatic, has been observed in some cases to lay eggs, in others to bring forth its young alive.

### III. *The Apodal Batrachians*

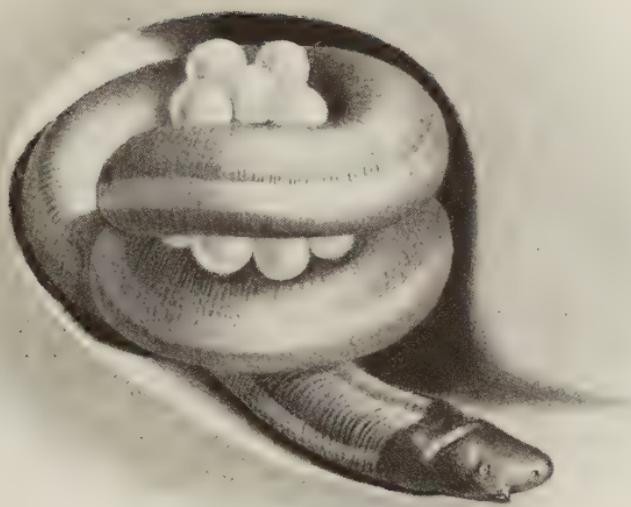
The burrowing, worm-like, limbless forms which constitute the Order *Apoda*, the Coecilians, have long escaped observation so far as their habits are concerned. Their mode of life and their habitat, confined to tropical lands, easily account for the fact that, although close upon fifty species are now described, we are more or less acquainted with the breeding habits of six

species only. As in the Tailed Batrachians, the female is fertilised internally, but, unlike them, a real copulation takes place, the male being provided with an intromittent organ very much like a penis, although morphologically representing only an eversion of the cloacal walls.

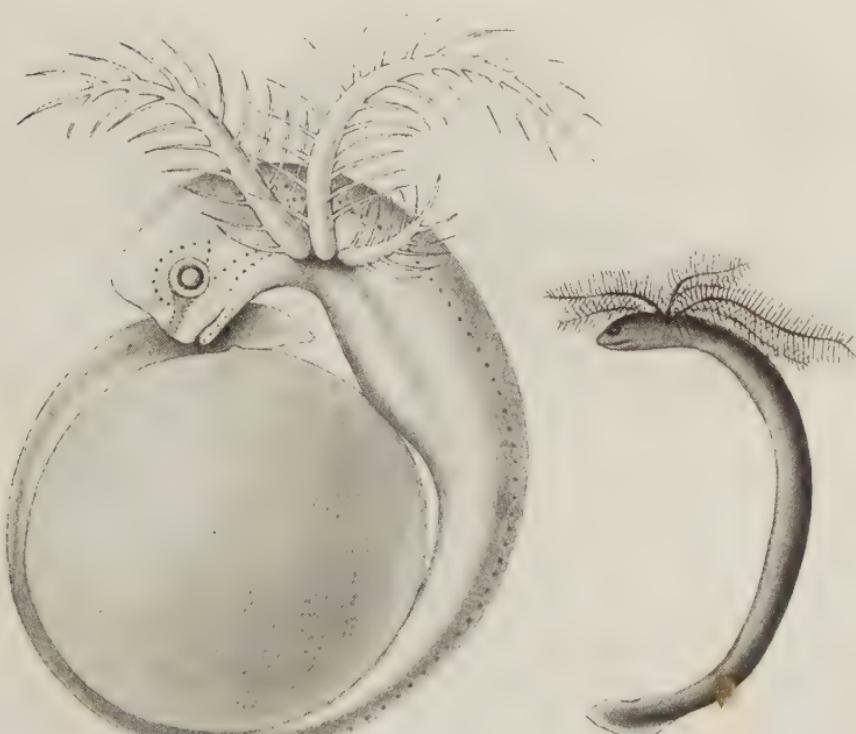
The breeding habits of *Ichthyophis glutinosus*, which inhabits South-Eastern Asia, have been observed in Ceylon. The female digs a hole close to the surface in damp ground near water and deposits about a score of large yellow eggs, measuring eight to ten millimetres in diameter. They are strung together in the same way as those of *Alytes* and *Cryptobranchus*, the connecting threads containing a very distinct twisted cord of the vitelline membrane, corresponding to the chalaza of birds' eggs, and form a bunch round which the mother coils her snake-like body, protecting them against enemies or possible desiccation until eclosion. (Plate XVII., A.) During this sort of incubation, the eggs enlarge, and within them the larva develops, coiled over the spherical vitelline sphere, and breathing by means of extremely long, delicately fringed external gills, three on each side. The gills shrivel and wither away before eclosion, the larva leaving the egg in a gill-less condition, but with a hole on each side of the neck, such as persists throughout life in *Amphiuma*, with small but well-developed eyes, and with a short but very distinct tail bordered above and below by a low fin. In this state it lives in the water like an eel, until it reaches a considerable size (70 to 160 millimetres). Later the hole on the sides of the neck closes up, the tail shortens and loses its fin-like crests, the eyes become covered over by the skin and very indistinct, and the animal lives on land for the rest of its existence.

Like those of *Alytes* and *Desmognathus*, the eggs were first believed to be truly meroblastic, but more recent investigation carried out on *Hypogeophis* render it probable that they belong to a modified holoblastic type which closely approaches the meroblastic.

In *Hypogeophis*, represented by two species in the Seychelles the development is on the whole very similar to that of *Ichthyophis*, but the young does not pass through an aquatic larval stage. It leaves the egg-capsule in the perfect condition and at once leads a terrestrial existence like its parents. In accord-



A WORM-LIKE AMPHIBIAN (*ICHTHYOPHIS GLUTINOSUS*): WITH EGGS



EMBRYO OF SAME TAKEN FROM EGG,  
MAGNIFIED

EMBRYO JUST BEFORE  
HATCHING, MAGNIFIED  
(AFTER SARASIN)



ance with the abbreviated development, caudal crests do not exist and the branchial aperture closes up as soon as the gills disappear; these are very similar to those of *Ichthyophis*, except that there are only two functional ones on each side, the third being quite rudimentary. The number of eggs in each brood varies between six and thirty. In the larger *H. rostratus*, the diameter of the egg varies between seven and eight millimetres, whilst in *H. alternans* it varies between four and five.

*Siphonops annulatus*, in Brazil, also lays its eggs on land, even in very dry localities, and nurses them in the same manner as the Coecilian mentioned above. They are only six in number and measure ten by eight and a half millimetres, when in an advanced state of development. The embryo has three large fringed external gills on each side.

Very little is known of the habits of *Typhlonectes compressicanda* of the Guianas and Venezuela, one of the largest Coecilians, reaching a length of 500 millimetres, but it appears to be more aquatic than most of its relatives. A female, found in the water, contained six advanced embryos of very large size, one of them being 157 millimetres long. These embryos breathe by means of two large flap-like membranous, external gills on each side, closely connected with each other.

*Dermophis thomensis*, from the island of San Thomé, Gulf of Guinea, is also viviparous, but appears to approach more nearly to the type of *Salamandra atra*. In the single gravid example examined, one uterus contained one young and the other two, and these young had neither gills nor gill-clefts, and but for size resembled the parent, except that the head was more distinct from the body, and the posterior part of the body was rather strongly compressed, as if for the purpose of swimming. These young measured about forty millimetres, the adult measuring up to 260.

These are the principal examples of the various modes of nursing and development with which we are at present acquainted in the three Orders into which living Batrachians are divided. But Nature does not easily reveal her secrets, and many are the surprises in store for future observers.

An inspection of the oviducts of many frogs and salamanders preserved in collections suffices to show that ova with large vitellus are the rule rather than the exception among those

living in tropical or subtropical countries. As such examples we may mention nearly all African tree-frogs (*Hylambates*, *Rapphia*, etc.), the curious African genera *Trichobatrachus* and *Gampsosteonyx*, the Solomon Island Frogs, *Cornufer solomonis* and *Ceratobatrachus guentheri*, etc. From the phylogenetic point of view the question naturally arises, which type of egg must be regarded as the most primitive. Some authors who have dealt with the question have expressed the opinion that the egg which is rapidly converted into the embryo, which afterwards undergoes a lengthy larval period in the water, has given rise by adaptation to the large egg, approaching the meroblastic type, in which the young frog, subsisting on a large supply of yolk, passes through part or the whole of the metamorphosis, whilst others, on the contrary, have argued that modern Batrachians are descended from land animals, and they have consequently regarded the forms dispensing with the metamorphosis as the most primitive. Most zoologists, however, hold that Batrachians are probably derived from fishes allied to the Crossopterygians and Dipnoans; as these fishes have eggs which are transitional between the extreme holoblastic and the meroblastic types, it seems rational to regard such eggs as the most primitive, and the extremes exemplified at both ends of the series by our common toad and by *Hylodes martinicensis* as derived from them.

From the evolutionary standpoint it is interesting to note the various steps by which the most aberrant modes of nursing are connected with the simple process of abandonment of the offspring. The first step consists in protecting the eggs by depositing them in a hole or under some shelter on land; further, the parents, or one of the parents, watch over the eggs, or coil themselves round them, this being followed by the actual transport of the eggs, with or without structural modification in the parent, such as brood-sacs. Again, we find the elaborate dorsal pouch of certain tree-frogs developed at different degrees, showing in what manner it may have been evolved. There is also every form of transition between the extreme holoblastic egg and one which is very nearly meroblastic.

The examples quoted above of species within the same genus, as in *Rana*, *Hyla*, *Nototrema*, differing so greatly from each other in their early stages strikingly show how the neces-

sities of environment may readily modify developmental processes and should teach us caution in using such characters for the interpretation of natural affinities. It is perfectly obvious that the structural and physiological features by which species may differ in their development do not always correspond to the system, based on a knowledge of the adult, on which a natural classification should rest. Forms undergoing metamorphosis have had a developmental history of their own, and larval forms such as tadpoles are outside the cycle of recapitulation, the ontogeny being broken by the intercalation of the larval phasis.

## CHAPTER V

### VARIATION AND ADAPTATION

Metamorphosis and occasional persistence of the larval condition (Neoteny). History of the axolotl and its explanation. Colour: protective and warning coloration. Adaptations for locomotion. Adhesive discs of tree-frogs. The spade of Pelobates. Respiratory adaptations: salamanders with neither lungs nor gills. Allantoic gills in embryos. Adaptations in the male for pairing. Convergent evolution in tree-frogs.

**I**N the commoner species, such as newts, frogs and toads, the young animal is hatched in the water as a larva, known as a tadpole. At the time of hatching the tail is still short, the mouth is indicated by a rhomboidal depression, but it has no opening, the anus is formed, there are branchial or gill-arches visible as transverse ridges, but no gill-clefts. On the first and second branchial arches on each side are small branched external gills. On the ventral surface of the head behind the mouth is a transverse crescentic groove bounded by ridges; this is the adhesive organ commonly but erroneously called the sucker; it has no muscles of suctorial action, but consists of cutaneous or skin glands, producing a sticky secretion which enables the larva to attach itself to the surface of leaves or other objects. After hatching it divides into two separate parts and at an early stage of larval life disappears altogether. When the mouth is formed it is not provided with true teeth, but has prominent lips which are marked with transverse grooves and the ridges between these grooves are developed into papillæ on the outer margin and more internally into several transverse series of minute horny teeth formed by the external horny layer of the epidermis. The jaws also within the lips are covered by a horny beak composed of similar teeth closely joined together.

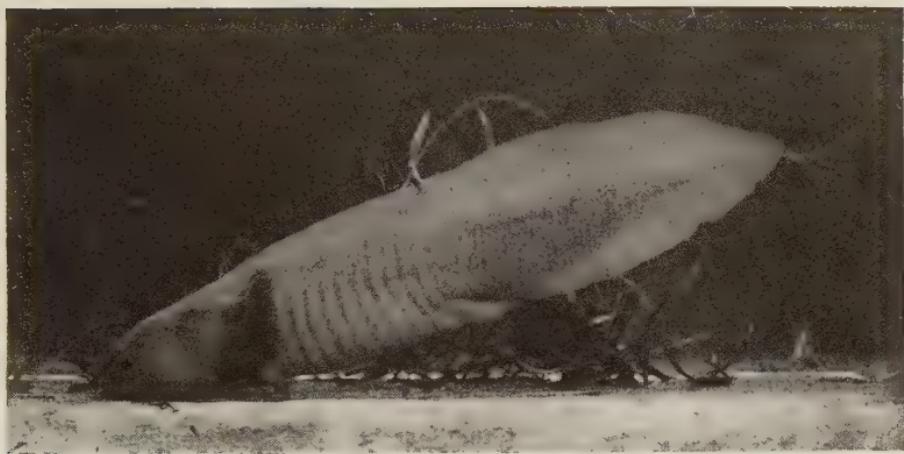
Four gill-clefts are formed and a third pair of external gills grow out on the third pair of gill-arches; the tail grows long and develops a median vertical fin-membrane. The paired limbs

are entirely wanting. This structure characterises what may be called the first stage of larval life. After about a week in the frog and its allies the second stage begins in which the external gills disappear and a transverse flap of membrane grows backwards from the hyoid arch and covers up the gill-clefts. This membrane is known as the "operculum," or "opercular fold". In the frog the posterior edges of the opercular folds unite with the skin of the body behind the gill-clefts leaving only a small opening on the left side. This aperture is sometimes called the spiracle, but it does not of course correspond to the spiracle of the shark-tribe which is represented in the frog by the tympanic chamber or ear-cavity ; the latter communicates with the throat by the Eustachian aperture but is closed externally by the tympanic membrane. In the tadpoles of the Aglossa, *Pipa* and *Dactylethra*, there are two "opercular apertures" one on each side, and in the Discoglossidæ the two lateral apertures unite into one which is ventral and median. In the tadpoles of the Urodela the operculum is always small and rudimentary, it extends only a short distance from the hyoid arch, and does not cover the external gills ; the latter are more dorsal in position than in the Anura and the opercular fold is sometimes continuous with the base of the first gill. The two opercular folds meet below the throat and often persist in the adult as a transverse ridge of skin known as the gular fold. Considering the structure of the gills, or branchial organs, in Dipnoi (lung-fish) and Crossopterygian (fringe-finned) fishes from which the Amphibia must have been originally descended, the rudimentary operculum in Urodela cannot be regarded as a primitive feature, but we must conclude that in the course of evolution the ancestral operculum has undergone divergent modifications in the Urodela and the Anura, in the former having been reduced, in the latter forming a closed branchial chamber with the exception of the small apertures above described.

Considerable difference exists between the Anura (frog-tribe) and Urodela (newts and salamanders) in the metamorphosis with respect to the limbs and tail. In the Anura the fore-limbs are at first concealed beneath the operculum, that on the left protruding through the branchial aperture, that of the right side actually bursting through the operculum. The hind limbs grow much faster than the fore-limbs ; although

they begin to develop at the same time the hind pair are at first alone visible because the anterior pair are concealed by the operculum. The limbs develop directly, first as cylindrical outgrowths and then becoming segmented into the parts of the terrestrial limb; they show no trace in their earlier stages of the structure of the fin of a fish. In the frog-tribe, when the hind limbs are well developed but small, the tail begins to grow smaller, but is not entirely absorbed when the frog leaves the water and becomes terrestrial. In the Urodela the only change which takes place in the tail is the partial or entire disappearance of the fin-membrane. In newts, which are species of the genus *Triton* or *Molge*, the fin-membrane is enlarged every season when the animals resume aquatic habits, and is reduced when they leave the water and lead a terrestrial existence. In *Triton* the fore-limbs appear much earlier than the hind. In the larvae of *Triton vulgaris* and other Salamandridæ there are a pair of tentacle-like organs situated just above the angle of the jaw on each side. They are little rods developed from the skin and have thickened ends; they are movable and are used chiefly to prevent the head from sinking into the soft mud at the bottom of the water; they are known as balancers. These organs occur also in *Amblystoma*, and in the larvae of the African clawed toad, *Xenopus* they are long, tapering and conspicuous. It is possible that the retractile tentacles of the Apoda correspond to these balancers.

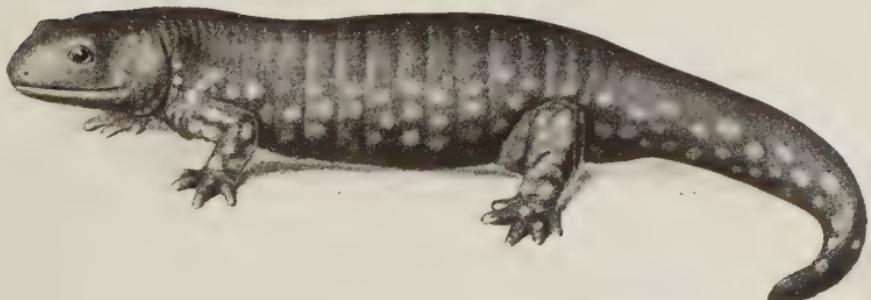
The lungs develop as a ventral "out-pocketing" of the throat behind the gill-clefts, dividing posteriorly into two sacs. Each receives an artery from the dorsal part of the fourth arch, and as the gill-clefts close up, the first arch forms the carotid arch sending blood to the head and brain, the second on each side remains connected with the dorsal aorta—the main artery of the trunk—while the third arch disappears altogether. In some cases and under abnormal conditions the transformation is postponed and the animal retains its gills and continues its aquatic respiration throughout life. The most remarkable instance of this is the celebrated axolotl. This creature is abundant in the lakes near the city of Mexico, it was found there by the Spanish conquerors of the country and was then and is still habitually used as food. The axolotl has three pairs of large external gills and four pairs of gill-clefts, the two pairs of



AXOLOTH, ALBINO SPECIMEN



INTERMEDIATE STAGE IN METAMORPHOSIS OF AXOLOTH



FULLY DEVELOPED *AMBLYSTOMA LIGRINUM*



limbs are well developed but rather slender, with five toes on the hind-foot, four on the fore-foot. The head is depressed with a somewhat pointed snout; the tail is compressed from side to side and has a broad fin-membrane which extends dorsally along the body almost to the neck. These axolotls reach a length of eight or nine inches or even sometimes as much as a foot; they are never known in the lakes near Mexico to go through any metamorphosis to a terrestrial condition, but pass their whole lives in the water and reproduce in the water-breathing condition. Originally therefore they were regarded as "Perennibranchiata" and under the name *Siredon pisciforme* were placed in the same division as *Proteus* and *Necturus*. In the year 1865 some axolotls which had been kept for a year in the Jardin des Plantes at Paris began to breed, the eggs which they laid hatched, and in six months developed into full-grown axolotls. This was complete confirmation of the belief that the axolotl was sexually mature in the gill-breathing condition, but this was not all: several of the young axolotls thus reared went through a metamorphosis, the gills disappeared, the clefts closed up, the fin-membrane disappeared, the head became broader and the animals left the water and became entirely terrestrial. It was thus shown that the axolotl was capable of changing into an air-breathing form which would naturally belong to the family Salamandridæ. It was therefore a probable conclusion that this terrestrial form was the species from which the axolotl was descended and that the latter was a larval form which for some reason had become permanent and sexually mature, but still retained the power of undergoing metamorphosis under suitable conditions. The most remarkable fact, however, was that the gill-less creature into which the axolotls were converted were not new, and unknown, but simply specimens of a well-known Salamandrine species which is common all over the United States from New York to California, a species named *Ambystoma tigrinum*. The Mexican axolotl is therefore simply the persistent and sexually mature larva of *A. tigrinum*; in other parts of North America the larva undergoes its metamorphosis while still small, and the animal does not become sexually mature until after this metamorphosis; in the Mexican lakes the larva continues to grow and breeds without passing through any metamorphosis at all. It is a curious fact that

only some of the young axolotls mentioned above as reared at Paris underwent the metamorphosis into *Amblystoma*, the rest, kept under apparently the same conditions, remained water-breathing axolotls.

Various theoretical explanations of the history of the axolotl have been maintained by evolutionists. The most extreme of them, namely that the change of the axolotl into the *Amblystoma* is a new evolution happening for the first time must be rejected at once, for a new form could not be expected to be identical with one already existing. The axolotl must have descended from normal *Amblystomas* and under certain conditions have reverted to its ancestral form. Weismann went so far as to maintain that the axolotl itself was to be regarded as a reversion to the original aquatic ancestor of the Amphibia, but we know that the larva in the possession of limbs of the terrestrial type differs essentially from the ancestral fish. We are thus forced to accept the view that the case is merely the loss of the adult stage of development and the persistence of the larval stage; this phenomenon has been called *neoteny* from *neos* young, and *teino* extend, the extension of youth, of the young state. The term, however, while expressing the facts, is no explanation, we have to consider what are the causes of the phenomenon. The case of the axolotl is not unique, it is known that the larvæ of other Urodela occasionally grow to a larger size and even become sexually mature without losing their gills; the larvæ of the spotted salamander usually metamorphose when four centimetres long but occasionally they reach a length of eight centimetres or about three inches in the larval stage; larvæ of Triton have been found eight or nine centimetres long with functional gills and sexually mature; in one lake in Lombardy such gill-breathing mature specimens occur constantly, affording an instance of a European axolotl. In the Anura also the larval stage may be prolonged, but no instance is yet known in which they become sexually mature in this condition. Further it has been shown that the metamorphosis of axolotls can be determined or prevented by forcing them to breathe air or preventing them from doing so. If they are kept in shallow vessels in water insufficiently aerated they begin to change into the perfect *Amblystoma*, if kept in deep water with plenty of oxygen they remain axolotls. Thus we

have the secret of the mystery, although the explanation may not be complete in all details. The metamorphosis of *Ambystoma*, and to a certain degree of all *Amphibia*, is partly due to heredity, partly to conditions. Usually the conditions in which the larvæ live are such that, as summer advances, the water, being in small shallow ponds or swamps, becomes reduced by evaporation, raised in temperature, and for this reason as well as from the presence of rotting vegetation deficient in oxygen : the larvæ are therefore forced to inhale air and so the development of the lungs and the reduction of the gills are equally promoted by the external conditions. There is also a hereditary tendency towards this special response to the external conditions with regard to oxygen. The structural changes are not directly due to the change of conditions but the hereditary tendency is called into action by those conditions. According to the present writer's views, which are not shared by many other zoologists, the facts are best explained on the theory that the metamorphosis was in the first instance the direct result of the change of conditions, repeated through many successive generations ; as time went on the tendency to the change of structure became hereditary and thus the same change produced much more result than in the beginning. Similar phenomena are presented by many other cases of adaptive changes occurring in development ; for instance, the assumption of the erect position in the human species. A baby walks on all fours like a monkey and has to learn to walk upright ; but it learns to walk on the hind limbs with great rapidity with a little practice because there is a strong hereditary tendency to the requisite structural changes. These changes, however, would not take place so rapidly nor so completely by the action of heredity alone, that is if the child were never allowed to practice equilibrium and progression in the upright attitude.

Now when in the case of amphibian larvæ the changes in external conditions with regard to oxygen do not occur the hereditary tendency is not stimulated, and on the other hand the functional stimulation of the gills and associated structures is continued. This necessarily happens when the larvæ live in large lakes of which the water is always saturated with oxygen, and it is in just such lakes that we find neoteny to occur. At first the metamorphosis may only be postponed to a later period

of life and then take place, but if the history of each generation has some hereditary influence on the next the neoteny itself would become hereditary until, after many generations, the metamorphosis would not take place at all and we should have the larval, that is to say, the gill-breathing stage, lasting throughout life as in the axolotl. At the same time the original hereditary tendency to the metamorphosis would not be entirely lost, but only latent, and thus when the original conditions to which the metamorphosis is related were restored, the metamorphosis would take place as it does in the axolotl. The conditions which produce neoteny affect the respiratory organs and there is no reason why they should prevent the development of the reproductive system; therefore the fact that the persistent larvae may become sexually mature requires no special explanation, especially in view of the fact that the reproduction of the normal adult form takes place in the water.

It has been urged as one of the difficulties in explaining neoteny by the influence of conditions that in a number of larvae living under the same conditions, whether in nature or in captivity, some are found to remain in the larval stage while others go through the metamorphosis in the normal manner. This fact, however, does not constitute any insuperable objection to the explanation offered above. In the first place this irregularity in the results did not occur in the experiments of Marie von Chauvin on the axolotl; she was able to cause the animals to change into *Amblystoma* or to remain in the condition of Axolotls as she pleased. In the second place when numerous larvae live in nature in a large body of water well supplied with oxygen, it is impossible to say that they have all been exactly under the same conditions, for it will be to some extent a matter of chance whether a given specimen rises to the surface and takes air more often than another, and although the larvae are living together the amount of stimulus applied to lungs or gills by free oxygen on the one hand or dissolved oxygen on the other, will differ greatly in different specimens. Lastly it must be remembered that individual differences occur in all animals in all characters, and therefore doubtless occur in the strength of the tendency to metamorphosis in Amphibian larvae. There is no evidence, however, that any individual is

incapable of being affected by conditions in one direction or the other.

Kollmann has shown that neoteny occurs in a large number of species and he distinguished between cases in which the metamorphosis is only temporarily postponed, the tadpoles passing through the winter in the larval condition and passing through their metamorphosis in the following summer, and cases in which the animal becomes sexually mature in the gill-breathing condition. It is a curious fact that examples of the first kind occur in Anura and of the latter only in Urodela. The following are the species in which neoteny has hitherto been observed : I. Partial Neoteny. *Pelobates fuscus*, *Bombinator pachypus*, *Pelodytes punctatus*, *Alytes obstetricans*, *Hyla arborea*, *Rana esculenta*, *Rana temporaria*, *Bufo vulgaris* and *B. viridis*. II. Total Neoteny. *Triton vulgaris*, *T. alpestris*, *T. cristatus*, *T. boscai*, *T. waltlii*, and *Amblystoma tigrinum*.

Dr. Hans Gadow of Cambridge University has recently studied the axolotl in its native habitat and in his charming book *Through Southern Mexico*, gives a most interesting description from his own observations of the conditions under which it lives at the present time. About four miles to the east of the city of Mexico is the Lake of Texcoco which at the time of the conquest by Cortes extended to the city itself. The original native city was intersected by canals, was in fact a city of lake-dwellings, and as the plain in which the city lies is surrounded by mountains with numerous streams running into the lakes the latter were liable to spread in extensive inundations. At present great drainage works keep the level of the water fairly constant and the city is situated on dry land. The water of Texcoco is brackish and during the dry season the land from which it retreats is covered with a saline crust. The lake is "a dreary waste of water only enlivened in the autumn by numerous waterfowl and it contains several kinds of small fish, but there are no axolotls in it, the saltiness of the water making it quite uninhabitable to any Amphibia. This fact effectually disposes of the suggestion made by Weismann that the axolotls were compelled to remain in the water because the surrounding shores were covered with a saline crust which would be fatal to the terrestrial form ; there could scarcely be a saline deposit on the

shores unless the water was also saline. About eight miles to the south-east of the city is the lake of Xochimilco and just beyond it another called Chalco. The level of these lakes is about ten feet higher than that of Texcoco, and they are filled with perfectly fresh water and surrounded by fertile meadows. Xochimilco is broken up by hundreds of small islands of various sizes separated by channels and canals; these are known as chinamps or floating gardens although they are not floating but rise from the bottom. Many of them are made artificially, floating masses of vegetation being fixed by stakes of willow and poplar which soon take root and grow, and then mud is ladled up from the bottom and spread on the mass until an island is made sufficiently firm for cultivation. The water teems with both vegetable and animal life, it is full of decomposing vegetable matter and swarms with insect larvæ, worms and the celebrated axolotls."

Dr. Gadow's conclusion concerning the reason for the axolotl remaining in the larval condition is as follows: "The unfailing abundance of food and water, the innumerable hiding-places for them in the mud, under the banks, and amongst the reeds, all these features are attractions so great that the creatures remain in their paradise, and consequently retain all those larval characters which are not directly connected with propagation. There is nothing to prevent them from leaving the lake and becoming land newts, but there is nothing also to induce them to do so." This does not seem to me altogether convincing or scientific. It is true that abundance of food may be one of the conditions which favours the retention of the larval organs and tends to postpone the metamorphosis, but the important point to consider is not that the animals remain in the water but that they are able to continue to breathe in the water. There are many Amphibia which are aquatic in the adult condition, for example *Pipa* and *Dactylethra* among the Anura and *Triton waltl* among the Urodela, and yet pass through the metamorphosis as usual and breathe air in the adult condition, rising to the surface to obtain it. Dr. Gadow himself proceeds to inform us that in the mountain streams of the Sierra de Ajusco, not far from the lake where the axolotls flourish, lives another species of *Ambystoma*, *A. altamirani*, which passes through the normal metamorphosis and becomes a lung-breather in the adult

condition, and yet like the axolotl it never leaves the water but is aquatic throughout its life, both in the gill-breathing and the lung-breathing condition. Nothing could prove more conclusively that the neoteny of the Axolotl is not due merely to the fact that it remains in the water, and it cannot be suggested that *Ambystoma altamirani* metamorphoses because it has less food than the Axolotl, for it finds enough food in the water, in its adult air-breathing state. Why then of these two species, both permanently aquatic, does one remain a gill-breather and the other change into a lung-breather? The question cannot be answered completely until the physical conditions under which they live respectively have been thoroughly analysed and compared; but there are indications in Dr. Gadow's description that the real explanation lies in the difference between the waters in the two cases with regard to the dissolved oxygen. Lake Xochimilco contains besides living plants a great deal of decomposing vegetable matter and this would naturally remove much oxygen from the water and give off carbon dioxide in return; but evidently since the water contains numbers of fish and larval insects it must be highly charged with oxygen. The lake receives few streams, but numerous springs of the clearest water rise up in various places from the bottom especially at the southern end where they are very deep; it is probable that these springs, whatever their origin, are saturated with oxygen and the lake would thus receive a constant supply of this element at the bottom, whereas in other cases, when oxygen is only obtained from the surface, decomposing vegetation in a warm climate removes all the oxygen from the deeper layers of the water. On the other hand, it is not so easy to find evidence that the water in which the larvæ of the metamorphosing species, *Ambystoma altamirani*, live, is deficient in oxygen. Dr. Gadow states that both larvæ and adults were found in June and September in the cool rushing streams, and such streams are not likely to be deficient in oxygen. Altitude might make some difference, these streams being about 8000 feet above the sea while the city of Mexico is about 7400 feet; not a very great difference. Dr. Gadow, however, remarks that the larvæ are not, like the adults, restricted to the clear streams, but lived also in quiet water which was muddy and overgrown with watercresses and similar plants; such water might very probably

be deficient in oxygen, and it is possible that both the streams and the quiet water become much reduced in the dry season, a point on which Dr. Gadow gives us no information.

The elements of coloration in the skin of Amphibia, especially of Anura are similar to those of the skin of fishes: they are of three kinds, black chromatophores, coloured chromatophores, and bodies composed of reflecting substance called iridocytes. Diffuse pigment also occurs and is usually yellow; the coloured pigment ranges in tint from yellow to red; as in fishes there is no green pigment, although tree-frogs, like many fishes, exhibit a distinct green colour. Amphibia, like fishes, have the power of changing their colour in accordance with their surroundings, a power which has been lost almost entirely by reptiles, birds and mammals; it is, however, retained by some reptiles and is highly developed in the chamæleons. The change of colour with change of surroundings is conspicuously seen in tree-frogs; when they sit on green leaves they are green, when they sit on brown bark they become brown. (Plate XIX., A.) Dr. Gadow describes how he received a number of *Hyla arborea* in a box with moss; when they were unpacked they were of a dull greenish-grey, they were placed in an enclosure with freshly cut branches of a lime tree, and next morning the leaves had withered and the frogs were at first invisible, but a closer examination showed that they were sitting on the dark brown branches and had turned to a light brown colour mottled with darker patches; this is an instance of variable protective resemblance. According to the researches of Biedermann the colour elements in this frog are a mosaic of polygonal iridocytes or interference cells and black branched chromatophores. The interference cells are stated to consist of a lower half containing white granules and an upper half containing yellow drops, although it has usually been found in fishes that the coloured chromatophores are distinct from the iridocytes. When the black chromatophores are expanded, the frog is of some shade of brown, when they are contracted the light passes through the yellow colour and then, being reflected from the white reflecting substance, by interference becomes green. According to Biedermann tree-frogs turn green when in contact with leaves even in a perfectly dark



A.—*HYLA BAUDINI*, A TREE-FROG OF NICARAGUA: AN EXAMPLE OF PROTECTIVE COLORATION

B.—*BOMBINATOR IGNEUS*, THE FIRE-BELLIED TOAD, SHOWING WARNING COLORATION AND WARNING ATTITUDE



vessel, or when blind, and in the same way they turn brown when on rough surfaces such as bark; he concludes that in frogs the chromatic function depends chiefly on sensory impressions received by the skin, while that of fishes depends on the eye. Gadow found, however, that in many cases the frog assimilates its colour to many other tints besides green and brown; one of his specimens rested during the daytime in a corner of a window-frame near putty and discoloured white paint and it became of a mottled leaden colour.

In the majority of Amphibia markings are not very definite or conspicuous; the green of tree-frogs is fairly uniform and in other cases there is nothing but an irregular mottling. A few exceptions occur in species which exhibit what is called warning coloration, that is conspicuous colours and markings associated with some poisonous or dangerous quality, and bold, fearless habits. One of the best examples of these characteristics is afforded by the spotted or fire salamander which is black with large irregular patches on the back and limbs of bright yellow or orange, the colours we see in a wasp; the lower surface is bluish-black. The animal is poisonous, producing a poisonous secretion from the glands in a thickened patch of skin behind the tympanic membrane on each side; there are also glands along each side of the back and on the flanks. The secretion is a milky white liquid which if it accidentally touches the human eye causes burning pain and inflammation; a few drops of the poison in the stomach or injected into the blood of a small animal are fatal. The parotid glandular patch is present in most of the Anura but the development and the activity of the poison vary greatly: the toad is much more poisonous than the frog, the latter being eaten by many other animals, the former being usually avoided, and if a dog bites a toad the poison causes great pain from its effect on the mucous membrane of the mouth. Among the Anura *Bombinator igneus*, called the fire-bellied toad, has the same association of warning colours and poisonous qualities as the spotted salamander. (Plate XIX., B.) In *Bombinator* the upper side is dark grey or nearly black and the warning colour is on the lower side which is black with large red or orange-red patches. It has often been stated that these toads when disturbed on land turn over on their backs, but this is not

the case, the animal remains in its normal position but turns its limbs over its back so as to show as much as possible of their lower surface and of the red markings of the belly. *Dendrobates* in South America offers an example of a tree-frog which instead of being protectively coloured like the Hylidæ is warningly coloured and poisonous: some are black and white, others black and yellow or black and red, one species is red with small dark marks on the back, and black legs. A very curious use is made in Brazil of the poison secreted by the skin of *Dendrobates tinctorius*: the feathers of the head and neck or other parts of green Amazon parrots are plucked out and the skin is then rubbed with the poison or simply with the skin of the living frog and as a consequence the new feathers which grow are yellow instead of green, so that artificially coloured parrots are produced, which are valued as curiosities. In Colombia the Indians are said to use the same poison for poisoning the tips of their arrows, which are employed especially for shooting monkeys. The poison acts on the heart and central nervous system.

The contrast between the lizard-like shape of the newts and their modes of locomotion and the structure of the frog or toad, adapted for leaping and destitute of tail, is very conspicuous. As in the original Amphibian the limbs were evolved from the fins of fishes by adaptation to terrestrial conditions, so in the Anura the elongation of the hind limbs for leaping and the loss of the tail could scarcely have been due to the requirements of locomotion in the water. At the same time both the Urodela and the Anura usually pass part of their lives in the water, and their different types of structure are adapted to both aquatic and terrestrial movement. In the Urodela when the animals are either temporarily or permanently aquatic the tail is furnished with a membranous fin; in the common British newts this fin diminishes greatly when the animals leave the water after the breeding season; in the salamanders which are almost entirely terrestrial, the fin is absent, as it is also in the genus *Ambystoma*. In some species there is a membrane along the dorsal edge of the body as well as on the tail; this is known as the crest and is confined to the males as in *Triton cristatus* and *vulgaris*. This crest occurs in those species which perform a lengthy courtship in the

water, while in forms that practise an amplexus, such as *Triton waltlii*, *T. asper*, etc., there is no crest. On the hypothesis of the inheritance of acquired characters this difference is explicable, the crest of the male being attributed to the effect of the pressure of the water in the active vibratory movements which the male continues for hours or days in presence of the female.

In the Anura the hind limbs are elongated in adaptation for jumping as in many other animals, such as the kangaroo, the grasshopper, and the flea. The segments of the legs are all elongated, including the tarsus (ankle) and the attachment of the pelvic girdle to the vertebral column is shifted far forwards so that the number of presacral vertebræ—the vertebræ in front of the sacrum—is reduced to nine or less. The effect of this is to place the application of the force of propulsion near to the middle of the body and so give greater efficiency. The hind toes are usually united by a web or membrane for the purpose of swimming in the water, the frog swimming with its hind feet, while the newt swims with its tail. In some cases the toes of the fore-foot are also webbed, but this seems not to be an adaptation for swimming, as in the most completely aquatic species such as the Aglossa *Pipa* and *Xenopus* the front toes are free, and the webbed condition of these toes occurs in arboreal species. In *Nectophryne*, a genus of the Bufonidæ occurring in Africa, India and the East Indies, the toes of both fore and hind limbs are webbed, and the species of this genus are believed to be arboreal, while in the allied species *Nectes subasper* of Java the fore toes are free and the animal is aquatic. Perhaps the webbing of the fore toes is always adapted for supporting the animal in the air during its leaps in the trees, as in *Rhacophorus pardalis* and other species of the same genus. *R. pardalis* was first described by A. R. Wallace in his *Malay Archipelago*. It was brought to him by a Chinese workman who said he saw it come down in a slanting direction from a high tree as if it flew. The feet are not only fully webbed, but much enlarged, so as to present a greater surface; this species lives in the forests of Borneo and the Philippine Islands; its total length is two and a half inches.

In the arboreal Anura the ends of the toes are expanded into adhesive discs by which the animal is able to attach itself firmly to the surfaces of leaves. It is a well-known fact that if

a specimen of the common tree-frog, *Hyla arborea*, is thrown against a pane of glass it sticks to the glass almost like a piece of putty, adhering by these discs. In the majority of cases, as in the Hylidæ and in *Ceratophyla* among the Cystignathidæ, the terminal phalanges which bear the discs are claw-shaped and bent upwards, their bases being enlarged. Between the terminal and the penultimate phalanx is a cartilaginous disc which projects ventrally and helps in the formation of the pad, which however is chiefly carried by the terminal phalanx. When not in use, as for example when the frog is sitting on a rough stone, the pad is round and turned upwards, and the phalanx is seen as a slight ridge on its upper surface; when the pad is adhering it is flattened and the phalanx is sunk into it. The pad contains unstriated muscular fibres the contraction of which produces one or more longitudinal grooves on the lower side. The adhesion of the discs is due not to sucker-like action, but merely to the attraction of two surfaces in close contact assisted by the viscosity of the secretion of the glands present in the skin of the discs. It has been shown by Schuberg that a glass disc of sixteen square millimetres in area merely pressed against the moistened under surface of a glass plate supported a weight of fourteen grammes while the weight of a frog having a similar amount of surface in all its discs together weighed only four grammes. On the other hand when there is an excess of moisture adhesion does not occur and a tree-frog cannot attach itself to thoroughly wet glass or leaves. In *Rhacophorus* among the subfamily Raninæ the terminal phalanges which bear the adhesive discs instead of being claw-like are bifurcated, and in the subfamily Dendrobatinæ, which are also Ranidæ modified for arboreal habits in South America and Madagascar, the terminal phalanges are T-shaped. Within the limits of South American Cystignathidæ we find similar differences in the shape of the terminal phalanges which carry the adhesive discs; in *Centrolene* they are bifurcated, in *Hylodes*, *Plectromantis* and others T-shaped. Possibly these differences may be due to the different positions in which the toes are habitually held in the different forms; it would seem that the discs in Hylidæ are developed at the base of the terminal phalanges, where the bones are bifurcated on the under sides and where the bones are T-shaped on the tips of the toes.

An interesting adaptation to the habit of digging occurs in the spade-footed toads of Europe, *Pelobates* and *Scaphiopus*. The inner tarsal (ankle) tubercle which occurs in Anura generally is developed into a curved oblique ridge covered with a hard horny sheath with a sharp edge; this organ is used as a spade or shovel with which the animal digs its way into soft soil, especially into sandy ground. The loose sand falls on the toad as it shovels away that which is underneath and so it sinks backwards into the ground quite rapidly and remains buried in the daytime, emerging at night in search of food. This is one of the cases which to a Lamarckian seems inexplicable except on the theory of the inheritance of the effects of external stimulations. We can scarcely doubt that if the feet were used for digging as they actually are used, the friction would cause a thickening and cornification of the epidermis at the part most affected, and if such effects were inherited the organ as it exists would be produced. The opposing view is that although in the individual the epidermis would be thickened and hardened, yet the evolution of the structure was due to the selection of spontaneous variations which were independent of the friction due to the act of digging.

The most surprising fact concerning the respiratory organs of Amphibia is the absence of lungs as well as gills in certain species of Urodela. These species all belong to the family Salamandridæ, in which the gill and gill-clefts are normally lost in the adult condition. The lungs may be entirely absent or reduced to a vestigial condition of no functional value. All the Desmognathinæ and Plethodontinæ, so far as known, are lungless and also *Ambystoma opacum* and *Salamandra perspicillata*. With the disappearance of the lungs are correlated certain changes in the circulatory organs: the pulmonary veins are naturally absent and the left auricle is much reduced in size and not completely separated from the right, so that the heart has practically only two chambers, one auricle and one ventricle, as in a fish. In all Amphibia the skin is an important organ of respiration and we know that in the hibernating condition the animals depend on the skin alone for the little oxygen which is required. According to one investigator the skin is the respiratory organ in the lung-less salamanders, but others maintain that the action of the skin is unimportant and that the

function is performed by the buccal cavity and pharynx. In *Autodax lugubris*, a lungless species which is common in California and which never enters the water, the throat vibrates rapidly, from 120 to 180 times per minute, drawing in and sending out air; since a frog breathes by forcing air into its lungs, raising the floor of the mouth while the external nostrils are closed, it is easy to understand that the same action carried on with the nostrils open would only drive air in and out of the mouth. In this case the lungs would no longer be used and would therefore in the course of evolution diminish and at last disappear or become vestigial and functionless. We see then that the loss of the lungs may have been caused by a very slight change in the respiratory movement. In *Speleperes porphyriticus*, which lives in the Alleghany mountains of North America, Dr. Gadow found that the respiration by movements of the throat was very limited, most of the oxygen required being absorbed through the skin which is very moist and slimy. This species is found only in wet places and is very sensitive to drought; when the skin becomes dry the animals show signs of suffocation and great discomfort.

The respiratory adaptations in the larvæ especially in those whose development takes place within the egg, not in the free state, are remarkably varied and interesting; the most important are described in the section dealing with breeding habits and development. It is curious to compare the various modes in which the larval stage is modified in Amphibia with the embryonic adaptations of reptiles, birds and mammals. In all these three classes the embryo is always provided with oxygen by means of the allantois, which is an outgrowth of the hind-gut. The Amphibia, on the other hand, although they possess in the urinary bladder which opens into the cloaca an organ answering to the allantois of the embryos of higher vertebrates, make no use of this structure as a respiratory organ. In the Californian newt, *Autodax lugubris*, in which the whole of the metamorphosis takes place within the egg, the external gills, instead of being branched or fringed, form on each side a broad three-lobed membrane of which the outer surface is applied to the inner surface of the egg-capsule, in this respect resembling the allantois of the higher classes. In *Plethodon cinereus*, on the other hand, in which also the gilled stage is passed within the gelatinous capsule of the egg,

the gills are long and branched. In the viviparous *Salamandra atra* the long gills of the embryo not only serve for respiration but also in the later stages of development absorb nourishment from the walls of the uterus, thus performing another function of the allantois which in the Mammalia is performed by the allantois. Somewhat similar allantoic gills, as they have been called, occur in the embryos of some species of *Notoptrema*, in which the whole development is passed through in the egg. In this case the gills envelope the embryo and are only connected to the gill-arches by narrow stalks. In other cases again, as in *Hylodes martinicensis*, in which also the development takes place within the egg, the gills and clefts have been lost altogether, and the organ of respiration of the embryo is the large and vascular tail. It may be pointed out here that when the tadpole is free and active in the water it is properly called a larva, but when the tadpole develops in the egg with more or less modification it becomes an embryo. All these different embryonic adaptations in Amphibia may be regarded as partially successful experiments as compared with the one method which, originally adopted by one group, has given rise to the reptiles, and has persisted with modifications in the birds and mammals which arose from them. This method consisted in the development of a large yolk, foreshadowed in some of the Amphibia, the formation of a tough usually calcareous egg-shell and the development of the amnion and allantois. The amnion is a growth of the outer membrane covering the yolk-sac, a fold of the membrane being formed which grows up and encloses the embryo dorsally. It is perhaps possible that the large yolk was the original cause in the development of both allantois and amnion, for the increase in the size of the yolk-mass necessarily involves a distension of the ventral region of the embryo, and an extension of the body-cavity ventrally: into this enlarged body-cavity the allantois is able to grow, and it may have been the growth of the allantois which originally pushed the amniotic fold before it.

The Amphibia present some interesting cases of adaptation in relation to the fertilisation of the eggs, and the protection of the young, that is to say, in structures related to the sexual and parental instincts. Some of these structures have been mentioned in the chapter on breeding

habits and development, but here they are to be considered specially from the point of view of evolution. In all cases where an amplexus of the sexes takes place the male is distinguished by modifications of the parts which are used in holding the female. A typical example of this occurs in the common frog, the male having a swollen tubercle on the inner side of the fore-foot covered with black skin, while the muscles of the fore-leg and the leg generally are larger and stronger than those of the female. The tubercle is pressed into the flanks of the female and the greater strength of the limb muscles enables the male to hold the female with sufficient power. The sexual instinct in male frogs is so great that occasionally they fix on to fresh-water fishes and blind them by pressing the tubercles into their eyes. These secondary sexual characters develop to a maximum in the breeding season and diminish very much afterwards, they are therefore sometimes termed nuptial organs. It has been recently shown that their development in the male and absence in the female depends on a chemical secretion produced by the testis and present in the blood. In a castrated frog these characters fail to develop, but if portions of testis from another frog are introduced under the skin of a castrated specimen the organs develop as in an uninjured frog. This fact supplies a new argument for the Lamarckian theory of the evolution of such secondary sexual characters, for it is possible that modifications originally due to friction of the skin or exercise of the muscles may produce internal secretions which act in the opposite direction on the reproductive organs. In all Anura which practise an embrace similar to that of the common frog there are similar modifications of the anterior limbs. In Urodela various modes of amplexus occur with corresponding modifications of structure. In *Diemyctylus viridescens*, an American newt, the male clasps the female with his hind legs either just before or just behind her fore-legs, and the hind legs in the male are larger than in the female, and in the breeding season hard rough black warts are developed on the inner surfaces of these legs. In the Pyrenean newt, *Triton asper*, the male holds the female by twisting his tail round the hinder part of her body, and the part of the tail used in this way by the male is larger and more muscular than in the female.

The most extraordinary of the adaptations for protecting

the young are the dorsal pouch in *Nototrema* and the united and enlarged vocal sacs in the little *Rhinoderma darwini*. In the former case the pouch is present only in the female and the eggs are probably introduced by the male; pressure of the eggs into the skin may from the Lamarckian point of view be suggested as the original cause of the formation of the pouch. In *Rhinoderma* the brood sac is confined to the male, and it is difficult to explain the origin of such a condition except as the result of the distension of the vocal sacs by the eggs. The male apparently developed the habit of taking the eggs into the mouth like the Cichlidæ among fishes, and thence they passed into the vocal sacs. The sacs are united, but they still open by two apertures into the mouth as in other Anura. When empty the sac only extends back to the pectoral region, but when filled with eggs it reaches to the groins and upwards to the dorsal surface, a truly extraordinary modification, sacs belonging to the mouth cavity acting as a brood-pouch and extending beneath the skin over the greater part of the body. The vocal sacs themselves in ordinary cases are at the same time an adaptation and a secondary sexual character; they serve as resonators to the voice which is produced by the larynx and in the breeding season the males are continually expressing their sexual excitement by their loud croaking, though whether this music has any effect in promoting the satisfaction of the sexual instincts may be doubted.

Regeneration, or recrescence, of lost parts, occurs in many Amphibia. This process is sometimes regarded as an adaptation evolved by natural selection, but to the present writer it seems more reasonable to regard it as a primitive property of the organism which tends to be lost with increasing specialisation of the individual. In Amphibia it is exhibited more strongly in the young stages; the gills and limbs of axolotls if cut or bitten off grow again, and this is true also of many or all Urodeles both in the larval and adult stages. *Proteus* reproduces a whole leg in about eighteen months, and in adult *Triton* the same complete recrescence has been observed. In Anura, on the other hand, recrescence of lost limbs is complete in tadpoles, but in the adult stages is slow and imperfect.

Animals of different lines of descent may become adapted

to similar conditions of life, and thus, although descended from different ancestors, come to resemble one another to a greater or less degree. Where the structure was originally fundamentally different the resemblances are only superficial and the essential differences are easily distinguished, as for example, when we compare a bat and a bird, or a whale and a fish. When on the other hand, the forms in question are originally somewhat closely related, and belong to the same group, adaptive convergence may produce a much greater similarity of structure, so that it is often difficult to distinguish such similarity from true affinity or community of descent. This is well illustrated by the Anura adapted to arboreal life, commonly known as tree-frogs. The arboreal species all agree in the possession of adhesive discs on the toes, which are necessary to enable them to cling to the foliage, but when we examine the internal anatomy we find that they often differ greatly from one another, and show affinities to different groups and to other species which may be aquatic, terrestrial, or burrowing. Although the discs have a similar structure and act in the same way, the structure of the terminal claws which support the discs differs considerably, as we have already seen, and the internal anatomy, such as the structure of the pectoral girdle, may be very different in forms equally arboreal. Thus the Hylidæ belong to the Arcifera and are therefore more closely related to the toads than to the true frogs, *Hylodes* belongs to another group, the Cystignathidæ, and the Dendrobatinæ are arboreal modifications of the true frogs or Ranidæ. According to Dr. Gadow this last subfamily itself is not a natural group, that is, not descended from common ancestors, but a convergent group. They have been separated from the other Ranidæ on account of the absence of teeth, but the fact that some occur in South America, and others in Madagascar and Africa, suggests that they are merely arboreal adaptations of the Ranidæ living in those different parts of the world. As Dr. Gadow puts it, it seems that the tropical forests must have tree-frogs, and these are manufactured in each region from the material that happens to be handy, that is to say, from the Anura that were already living in the region. Tree-frogs are therefore not all related together, but those of each region are most closely related to the other Anura of that region.

## SECTION III

# FISHES

### CHAPTER I

#### INTRODUCTORY

Definition. General Characters. Position in the Animal Kingdom, and Classification.

OF the myriads of animals, belonging to widely different types of structure, which live in the sea and the fresh waters, fishes are the most perfectly adapted to motion in the liquid medium. Many marine animals are fixed to the sea-bottom, like the corals and sponges, or crawl about on it, like the star-fishes, sea-urchins, and their allies ; others again merely float passively in the water, drifting with the tides and currents, like the jelly fishes ; others, although they have organs of locomotion, have them only in the form of lateral appendages, like some marine worms and the Crustacea, and cannot swim with any great speed. Some of the squids and cuttle-fishes, belonging to the class Cephalopoda of scientific classification, approach nearer to fishes in their powers of aquatic locomotion, the free-swimming or pelagic forms of this type having elongated bodies provided with lateral fins, by which they are enabled to move easily and to change the direction of their movements at will ; but they are far inferior to the fishes in their mastery of their medium.

Fishes possess the fusiform or spindle-like shape which is mechanically best suited to motion through water and their jointed backbone and powerful muscles afford them the most efficient means of propulsion. They realise in fact the mechanical conditions which human ingenuity has evolved in the screw-propelled steam-ship ; the hull of the vessel in the submerged part, and more completely in the submarine, is similar in shape to a fish, but as no revolving motion of one part on

another is possible in a living organism, the propulsion of the fish is effected by vibratory movements of the hinder portion of the body; the fins are flat, fan-like outgrowths which aid or direct the movement. The tail, or to be more exact, the caudal fin offers the necessary resistance to the water in the propelling motion, and acts like an oar used in the to-and-fro movement of sculling from the stern of a boat; in the forward part of its movement it is narrowed by the approximation of its rays and turned sideways so as to offer the least resistance to the water, while in the backward movement it offers the greatest surface and the greatest resistance. The caudal fin is vertical, and on the dorsal and ventral edges of the body there are other vertical fins which are median and unpaired, and whose function is to prevent the fish from turning over to one side or the other. The lower part of the body behind the head is enlarged to contain the digestive and reproductive organs and the surface of this abdominal region is broad and rounded and destitute of vertical fins; in this region, there are, however, two fins on each side, generally horizontal in position, and corresponding to the fore and hind limbs of the backboned animals which walk on land; the function of these fins is chiefly to preserve the position of the body and to control the direction of the movement; they are called the pectoral and pelvic fins, the former being close behind the gills, the latter in the more primitive fishes near the anus. The marine animals which most resemble fishes in their organs of locomotion and form of body and which come nearest to them in their mastery of the aquatic medium are the Cetacea or whales, but these are inferior to the fishes by the fact that, being in all essential respects similar to the hairy milk-giving vertebrates or mammals, they are still dependent on the air for respiration and are therefore compelled to rise to the surface at intervals to breathe. In consequence of their apparent resemblance to fishes in form and habits, Cetacea are popularly regarded as fishes but that they true mammals is proved by the facts that they have traces of hair, that they breath air by lungs, and that they suckle their young.

In fresh waters many of the marine types are entirely unrepresented, and on the other hand some aquatic creatures are found belonging to groups which include no marine species.

For example, there are aquatic insects of many kinds, and members of the class Amphibia such as newts and frogs, which either temporarily or permanently live in lakes, ponds, or rivers. Many of these, like whales and porpoises, are still dependent on the air for respiration, they are entirely unable to obtain the oxygen which is necessary for life from the water, and must therefore rise to the surface at frequent intervals, and none of them can move in the water with the grace and agility of the fishes.

Fishes may be generally defined as vertebrate animals which breathe in water by means of gills situated on the sides of slits or clefts leading from the cavity of the throat to the surface of the skin, and which possess paired and unpaired fins supported by fin-rays. If we consider the true or typical fishes we may add to the definition the possession not merely of a backbone or vertebral column but also of a skull, and not only of a skull but of distinct jaws placed transversely to the length of the body and hinged at the angles. The Lampreys and their allies resemble fishes in their breathing organs and in the possession of a skull, but they have no transverse jaws, the mouth being circular and suctorial, and no paired fins. The *Amphioxus* or Lancelet differs still more in the absence of jaws, fin-rays, vertebræ, and skull. Fishes are in many respects similar to Amphibia, especially when we consider the lung-fishes or Dipnoi which breathe partly by means of lungs, and certain Amphibia which retain gill-slits throughout life. The only character which separates all Amphibia without exception from all fishes is the absence of fin-rays in the former.

The structure of fishes must now be considered in greater detail. In general the more primitive condition of the organs is found in the sharks, dog-fishes, and rays (*Elasmobranchii*), and the common small ground dog-fish, *Scyllium canicula*, is a good example of such fishes, while the gold-fish or perch is equally typical of the scaly and bony fishes (*Teleostei*). The first part of the skeleton to be developed is a cylindrical unjointed rod of gelatinous tissue which runs through the axis of the body, and is technically termed the notochord. The formation of this structure is the first step in the development of the skeleton in the embryo fish, or indeed in the embryo of any vertebrate, and the segment of the spinal column or "vertebræ" are developed

not from it but around it. The tissue surrounding the notochord grows inwards at regular intervals so as to form rings which press into and constrict the notochord. The substance of these rings develops into cartilage, and the rings themselves become the bodies or "centra" of the vertebræ, which are hollow at each end like a dice box, so that the gelatinous substance of the notochord persists in the adult dog-fish between the "centra".

From the centra dorsally (Fig. 18) there extend processes called neural arches which enclose the spinal cord, and between the neural arches are intervertebral plates; in the middle line above are small pieces called neural spines; at the sides ventrally in the abdominal region of the body the centrum projects



FIG. 18.—Skull and gill-arches of Dog-fish (*Scyllium canicula*) with anterior part of vertebral column. *n.a.*, neural arch; *i.p.*, intervertebral plate; *o.c.*, olfactory capsule; *a.c.*, auditory capsule; *u.j.*, upper jaw; *l.j.*, lower jaw; *hy*, hyoid arch; *br. 5*, fifth branchial arch.

into transverse processes, attached to which are slender ribs. All these parts are composed in the dog-fish of cartilage, to some degree hardened by the deposit of lime, but not having the structure of true bone; in fact all the internal skeleton of this group of fishes is cartilaginous, whereas in other fishes it is replaced by bone. Attached to the anterior end of the vertebral column is the skull which consists of an undivided capsule of cartilage; in it can be distinguished the brain case in the median position, and two pairs of capsules at the sides, the anterior pair enclosing the olfactory organs and the posterior pair the auditory organs; at the sides between these capsules the skull is hollowed out to form the orbits in

which the eyes are contained. Beneath the skull and the anterior part of the vertebral column are a series of transverse bars of cartilage called the branchial arches (Fig. 18 *br.* 5) because they support the partitions or septa between the gill-clefts. The most anterior of these arches form the jaw cartilages ; these may be considered as one pair of which the lower half forms the lower jaw while the upper half forms the upper jaw. Posteriorly the articulation of the two is attached to the lower end of the first segment of the next arch, called the hyoid (Fig. 18 *hy.*) while anteriorly the upper jaw is attached to the lower surface of the skull. This mode of suspension of the jaws is highly characteristic of fishes, and occurs in the great majority of the shark-like forms as well as in the bony fishes. In a few cases, however, the upper jaw is firmly united to the skull and the lower jaw is articulated to the upper without the aid of the hyoid arch ; for example, in the lung-fishes (Dipnoi) and Chimæroids. All terrestrial vertebrates in this respect resemble the lung-fishes. Behind the hyoid arch are five branchial arches each segmented into several pieces. The rest of the internal skeleton consists of the cartilages supporting the paired and unpaired fins. Each unpaired fin, excluding the tail fin, is supported by a series of parallel rays, of which the internal segments called the basals are within the surface of the body, while the external parts, called the radials, are in the projecting part of the fin. In the posterior part of the caudal fin the basals cannot be separately distinguished, the radials articulating directly with the vertebræ. The terminal part of the vertebral column is bent upwards and the ventral basals and radials are larger than the dorsal, thus the ventral lobe of the tail-fin is the broader and the tail is said to be heterocercal. The pectoral fins are articulated to a transverse bar of cartilage called the pectoral girdle which passes across from one side of the body to the other ventrally ; the part below the articulation is called the coracoid cartilage, the part above it on each side is the scapula. The fin itself has three basals, of which the posterior is the largest, and the external part of the fin-skeleton consists of segmented radials diverging from the base. The pelvic girdle is smaller and there is only one long basal cartilage to which the radials are attached in parallel series.

Quite distinct from this cartilaginous endoskeleton are the calcified structures in the skin which form the external skeleton, or as it is technically termed exoskeleton. In the dog-fish these consist of small tooth-like structures which are called dermal denticles, that is to say skin-teeth. The skin of the fish, as of other vertebrates, consists of two layers, an outer cellular layer without blood-vessels, the epidermis, and a thicker internal layer, the derma, which is fibrous and supplied with blood-vessels. The dermal denticles are situated in the derma; each consists of a flat base having the structure of bone and a pointed spine projecting backwards and outwards. The external layer of the spine consists of enamel which is secreted at the inner surface of the epidermis; below it is a layer of dentine or ivory, the characteristic substance of teeth, and within this is the tooth cavity containing vascular pulp and opening by an aperture in the basal plate. These denticles have the same structure as the teeth in the jaws, and the teeth of other vertebrates are essentially similar. On the surface of the body in the dog-fish the denticles are everywhere arranged in regular oblique rows; in other cases they may be much larger in certain regions and absent in others, as for example in the skates and rays. In other fishes the points of the teeth disappear everywhere except in the jaws, and the teeth themselves are modified into flat bony plates in the skin, covered on the outer surface with a smooth layer of substance resembling dentine, and called ganoin. These ganoid scales may form a complete armour over the body and head, as in the Bony Pike (*Lepidosteus*) of North America (Plate XX., C); such fishes are often called ganoid fishes. Such plates over the head and pectoral girdle come into intimate connexion with the internal skeleton, which in bony fishes is ossified also into distinct bones. In the most specialised fishes like the gold-fish, which are called Teleostei, the dermal plates lose their outer layer of enamel and on the head and pectoral girdle form the superficial bones of the skull and fin-girdle, while on the body they are modified into the thin overlapping scales, which may be either smooth-edged or cycloid as in Fig. 20, A, or may have the exposed posterior border furnished with small spines as in Fig. 20, B. Thus in the bony fish the skeleton consists of the ossified internal skeleton united in the head and pectoral girdle with bones derived from the external skeleton

of the skin; these bones are known as dermal bones or membrane bones, and many of them persist in the skull and pectoral girdle of the higher terrestrial vertebrates. Thus we have the

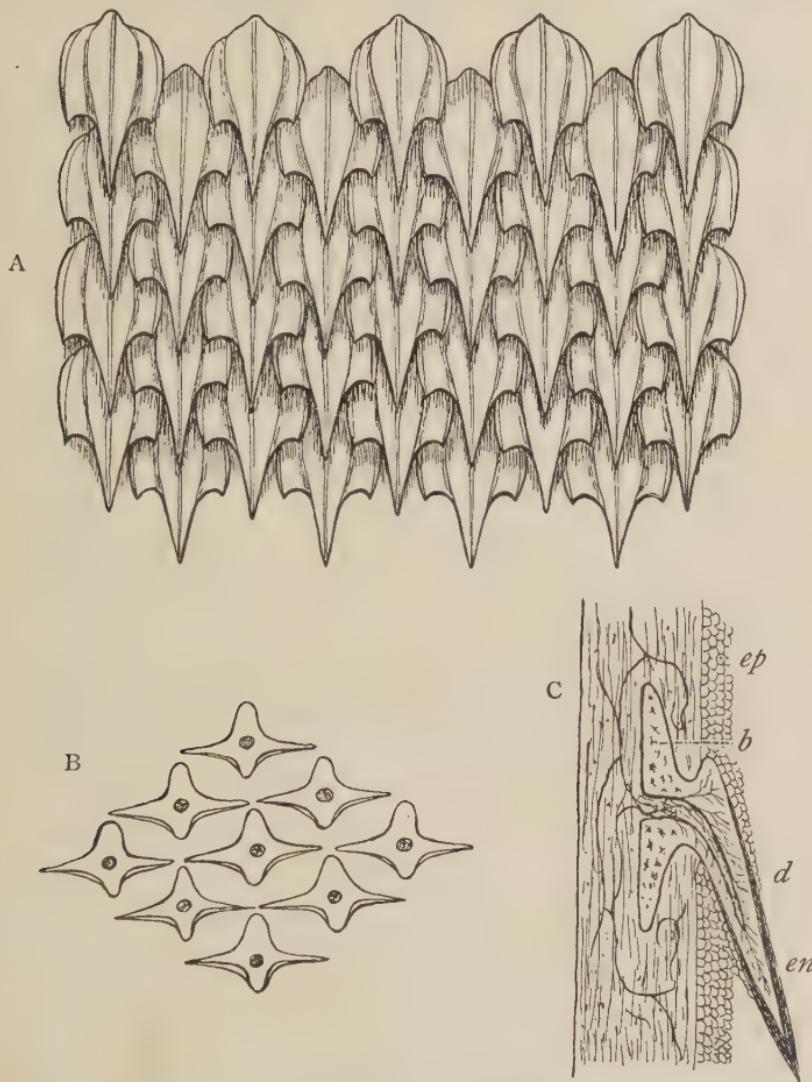


Fig. 19.—Dermal denticles of the Dog-fish (*Scyllium canicula*). A, from above; B, from below; C, in section; *b*, bony base; *d*, dentine; *en*, enamel; *ep*, epidermis.

remarkable fact that the frontal and parietal bones of the human skull are originally derived from the bony scales on the head of fishes, and at a still earlier stage of evolution from the dermal denticles on the skin of the head of the shark-like

ancestor, so that the frontal bone and the teeth were originally of the same nature.

There are also dermal fin-rays in addition to the rays belonging to the internal skeleton above mentioned. In the dog-fish and its allies the dermal rays are extremely fine and numerous fibres of horny character, situated in the skin on either side of the fin, and the denticles extend over the surface of the skin outside them. In the bony fishes the horny fibres are not present, but there are dermal rays which are really modified scales. In these fishes the internal skeletal rays are much shortened and reduced in the median fins to mere nodules while the fin is supported chiefly by the dermal rays. The

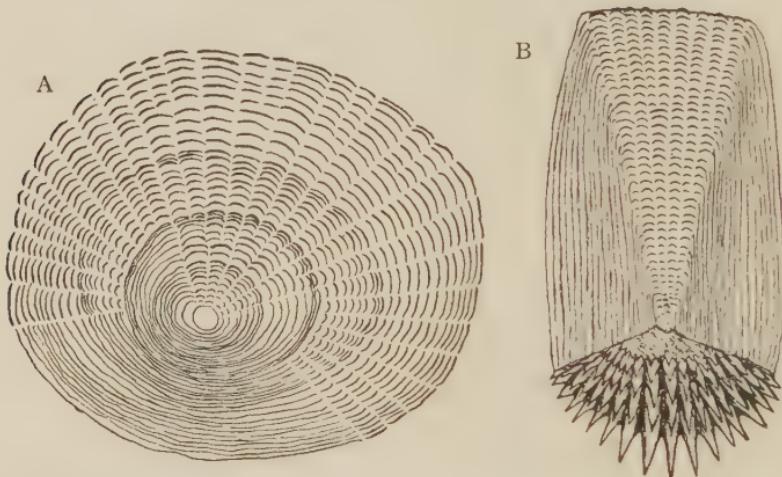


FIG. 20.—A, cycloid scale of Plaice, showing four zones of annual growth ; B, ctenoid scale of Sole.

latter are necessarily double as they are developed in the skin of both sides of the fin, and at their bases they bestride the ends of the internal skeletal radials. The basals persist as bones which alternate with the spines of the vertebræ and are therefore called interspinous bones, and in some Teleosts the reduced segments of the radials are united to the basals so that the dermal rays articulate directly with the ends of the interspinous bones. The caudal fin in Teleostei undergoes an interesting modification from the heterocercal structure which, as described above, is seen in sharks and dog-fishes. The dorsal upturned end of the vertebral column is reduced and converted into a single rod-like bone called the urostyle ; the ventral

spines of the vertebræ in front of this are enlarged, those at the lower angle of the tail being longer so that the posterior edges of these bones are in a vertical line, and the dermal rays articulating with these posterior edges form a fin which is outwardly symmetrical although all the rays except a few small ones at the upper angle are below the axis of the vertebral

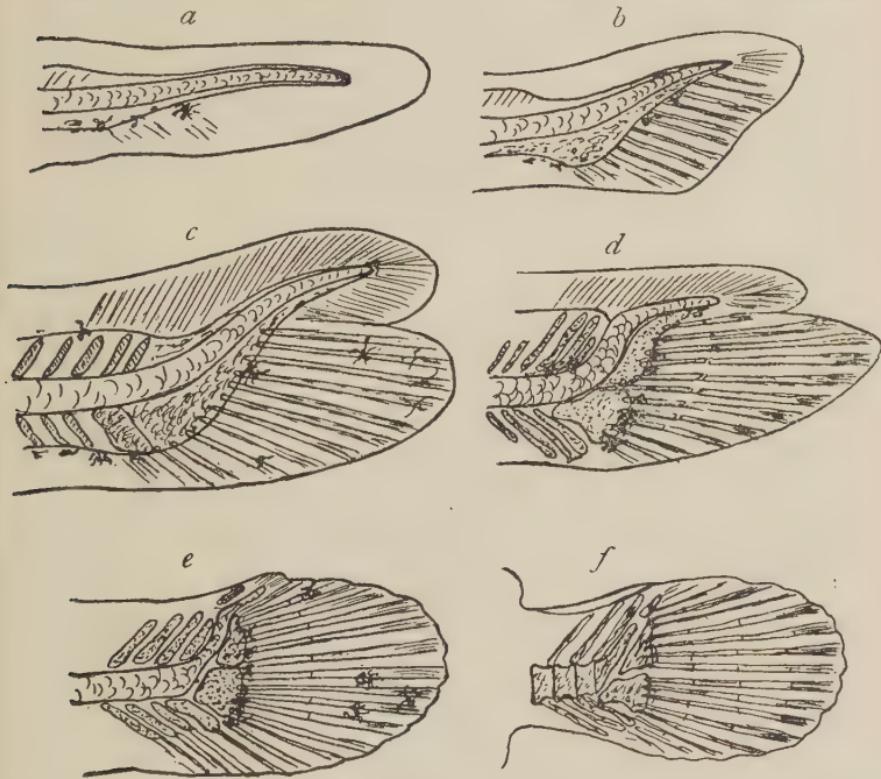


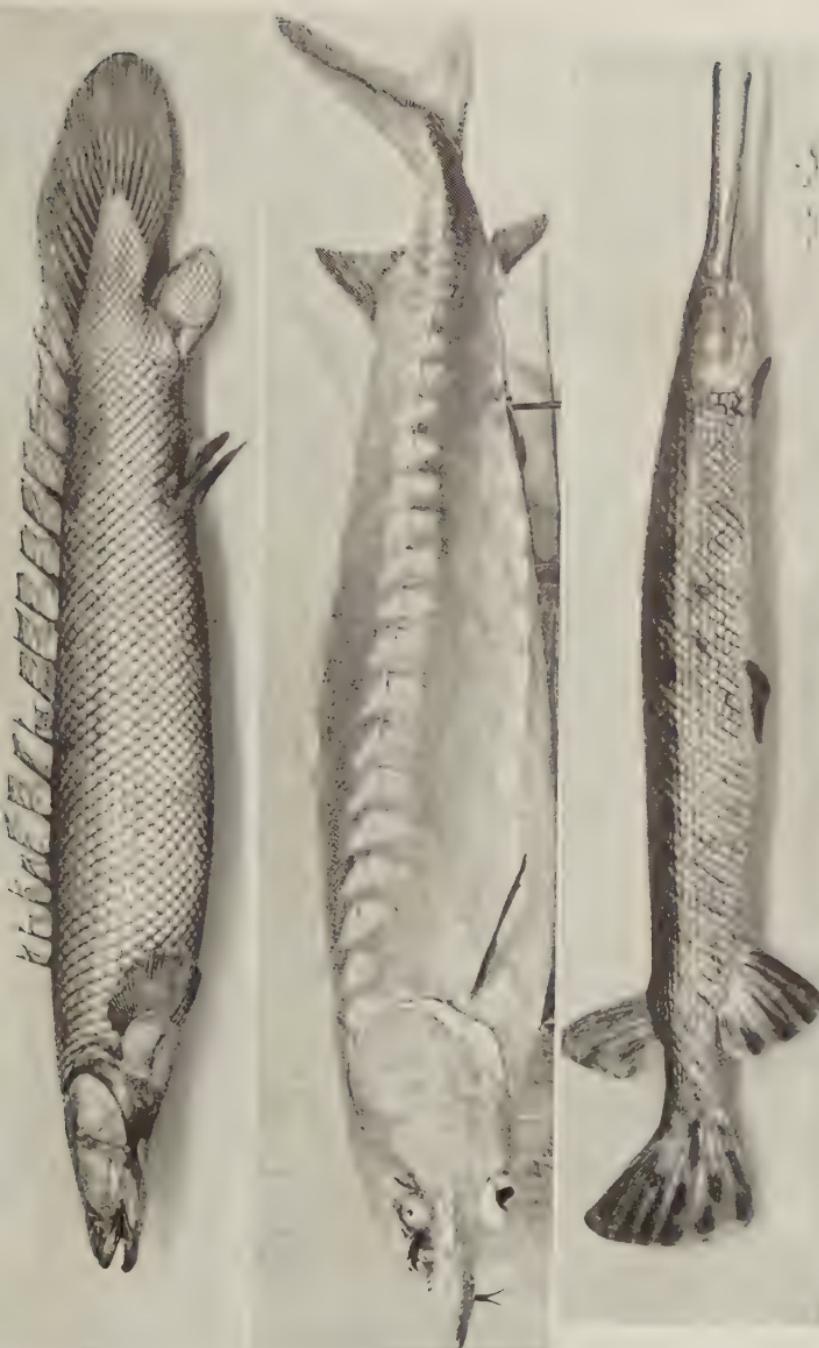
FIG. 21.—Development of the homocercal tail as seen in a young flat-fish. After Alex. Agassiz. *a*, youngest stage, almost symmetrical, without fin-rays; *b*, end of notochord slightly up-turned, dermal fin-rays appearing on ventral side; *c*, *d*, end of tail more bent up and reduced: *e*, *f*, the ventral rays become terminal.

column: a tail of this kind is described as homocercal, and is seen in Salmon, Gold-fish or Mackerel. In the development of a bony fish from the newly-hatched stage or larva, the tail-fin passes through stages which repeat the stages of its evolution (Fig. 21); the first signs of skeletal structures in the membrane are delicate hair-like rods representing the horny fibres of the dog-fish, then the end of the notochord becomes bent up and the fin-rays begin to appear on the lower or ventral side, thus forming a heterocercal tail (*b*.); then by the growth of the

ventral rays, the original terminal part becoming more bent upwards and reduced, the ventral lobe ultimately forms nearly the whole of the tail, is directed posteriorly, and acquires its new symmetry. On the other hand, in the cod family the tail is really and not merely apparently symmetrical ; it consists of equal numbers of upper or dorsal and lower or ventral rays, and the axis of the vertebral column is continued through the centre of the tail, not bent up to the dorsal angle as in the homocercal tail. This symmetry in the cod, however, is not primitive, but is due to the loss of the original heterocercal tail, and the meeting of dorsal and ventral fins at the end of the vertebral column.

The endoskeletal supports of the paired fins likewise undergo reduction in the bony fishes in increasing degree as we pass from the Ganoids to the Teleosteans. The pectoral girdle is reduced in the latter to two small bones called scapula and coracoid, and these are attached to the inner side of a series of dermal bones which perform the function of a pectoral arch. The most primitive Ganoids, called for this reason Crossopterygians, have the endoskeletal basals and radials well developed, as in sharks, and supporting a fleshy lobe fringed with the dermal rays (*crossos* means fringe). In other bony fishes the basals and radials are reduced and the dermal rays appear to rise from the base of the fin. There are no dermal bones in the pelvic girdle, the original girdle is much reduced, and the original basals form a single bone. One of the most curious modifications in Teleosteans is the change in position of the pelvic fins, which have moved forward so that they are in the most specialised forms either below or actually in front of the pectorals ; their skeleton is in these cases actually attached to the pectoral girdle, for example in the perch or cod. In such fishes, therefore, we have vertebrate animals whose hind limbs are on the same level or actually in front of their fore limbs. A cod, for example, may be truly said to have its hind legs attached to its throat.

The gill-clefts in the dog-fish and its allies open separately on the surface of the skin and are separated from each other by broad partitions or septa, at the inner borders of which are the cartilaginous gill-arches. The internal openings of the gill-clefts lead into the cavity of the throat, or as it is technically



A.—THE AFRICAN LUNGFINNED GANOID, *POLYPTERUS MACULIR*  
B.—COMMON STURGEON, *ACIPENSER STURIO*  
C.—AMERICAN BONG-PIKE, *LUTTUS LUTTUS* (L.)

A

B

C



termed, the pharynx. This connection between the nutritive apparatus and the respiratory organs is highly characteristic of Vertebrates, and when it exists in other animals is considered to be conclusive evidence that they are related by descent to the true Vertebrates, that they are in fact more or less remote cousins of the latter tribe, owing the common possession of this and certain other characters to descent from some common ancestor which existed at an early period of evolution. The gills themselves are ridges of the membrane on the anterior and posterior faces of the septa; there are four of these septa

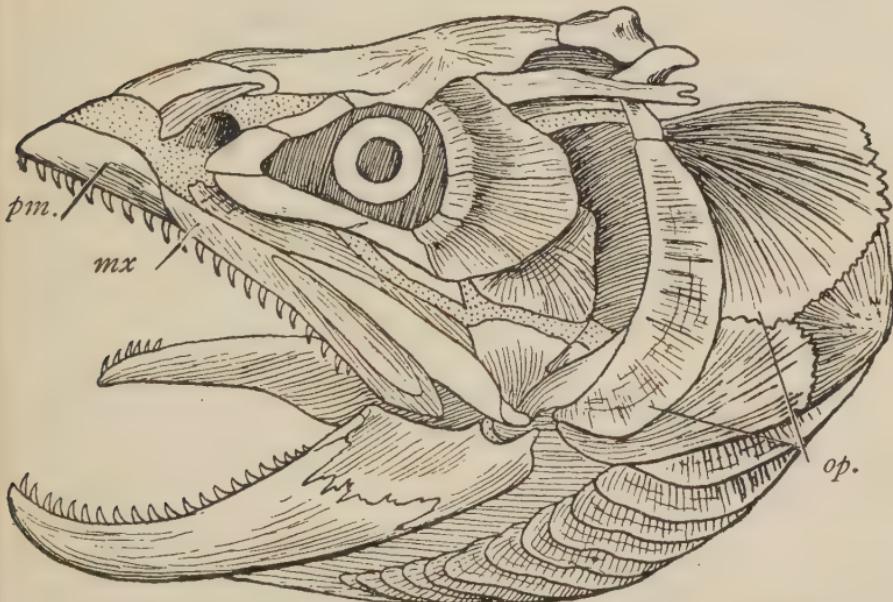


FIG. 22.—Skull of Salmon. *op.* opercular bones; *pm.* premaxilla; *mx.* maxilla.

with a series of gill-folds in front and behind; there is also a series on the posterior face of the hyoid but none on the anterior face of the last gill-arch behind the last cleft. In front of the hyoid is a reduced cleft called the spiracle. In the bony fish dermal bones are developed in front of the original upper jaw, on the lower jaw, and on the hyoid arch. Those in front of the mouth, called the maxillæ and premaxillæ, form a new upper jaw in front of the old one, and bear teeth. In the lung-fishes, this new jaw divides the aperture of the organ of smell into two external nostrils in front of the mouth and posterior nostrils inside the mouth, an arrangement which persists in

Amphibia and all terrestrial vertebrates. In bony fishes the posterior nostrils have closed up, and the external nostrils are again divided into two small apertures. The skin of the hyoid arch grows out into a flat plate, the gill-cover or operculum, which covers all the gill-clefts, leaving only one external aperture; the operculum is supported by several flat, broad, dermal bones (Fig. 20, *op.*). The broad gill-septa are reduced to narrow bars from each of which project two series of gill-filaments corresponding with the gill-folds of the Elasmobranch; the hyoidean gill-series becomes rudimentary, and is called a pseudobranch. There are thus said to be four gills in the bony fish, a gill being the gill-bar with its double series of filaments, and these gills can be seen as four red fringes beneath the gill-covers in any common fish.

The heart of the fish consists of one auricle and one ventricle, and it is situated in a special cavity called the pericardium, just behind the gills and ventral to the pharynx. The ventricle is triangular in shape, and from its apex, which is anterior, passes forwards the main artery which carries the blood towards the gills and which is called the ventral aorta. In the dog-fish the ventral aorta is elongated and the part nearest the ventricles is muscular and contains several transverse rows of valves; this part is called the truncus arteriosus. In the bony fishes the aorta is shortened and the truncus arteriosus is reduced, until in the Teleosteans there is no truncus arteriosus but only a single row of valves and beyond them a small dilatation called the bulbus arteriosus or aortic bulb. From the ventral aorta or aortic bulb are given off on either side the "afferent arteries" which convey the blood to the fine blood-vessels or capillaries of the gills; "efferent arteries" convey the blood from the gills to the dorsal side of the pharynx where they unite to form the carotid arteries anteriorly and the dorsal aorta posteriorly; the former convey the blood to the head and brain, the latter gives off branches to the various parts of the body including the digestive organs. In its passage through the gills the blood absorbs the oxygen dissolved in the water and gives up the carbonic acid or carbon dioxide which it has absorbed from the tissues. The respiratory movements of the mouth and pharynx take in water by the mouth and expel it through the gill-clefts, so that the water in contact with the gills is con-

tinually renewed. The veins which return the blood to the heart all unite, with the exception of those from the liver, into two transverse veins called the Cuvierian veins, which meet together at their opening into the auricle; there is no posterior vena cava as in higher vertebrates. The hepatic veins open directly into the sinus venosus formed by the union of the Cuvierian veins.

In the digestive organs the points of difference from those of other vertebrates are not of great importance. The narrow gullet is the continuation of the pharynx and opens into the stomach. The short and wide intestine provided internally with a spiral valve is characteristic of Elasmobranchs and the valve disappears in the Teleostei. In the latter also the pancreas is reduced or wanting and its function is probably performed by a number of short tubes opening into the beginning of the intestine, and known as the pyloric caeca. In the nervous system the brain is chiefly distinguished by the great development of the cerebellum and the small size of the cerebral hemispheres in most fishes; the hemispheres are less developed in Teleosteans than in Elasmobranchs, but in the Dipnoi, on the other hand, they are large and well-developed. The three chief pairs of sense organs, olfactory sacs, eyes, and auditory organs, are present. The olfactory sacs are a pair of simple depressions or invaginations of the epidermis opening in front of the mouth; the division of the opening by the dermal bones of the upper jaw has already been mentioned. The eyes have a flatter cornea and a more spherical lens than those of terrestrial vertebrates; in Teleosteans there is a special layer of reflecting tissue, composed of a chemical compound called guanin, behind the retina. The auditory organs are membranous sacs entirely enclosed in the auditory capsules of the skull, each is divided into an upper part provided with the usual three semicircular canals and a lower part called the sacculus; opening into the latter is a narrow tube which is the vestige of the epidermic invagination by which the auditory sac is formed in development; for the organ of the sense of hearing like that of the sense of smell is nothing but a portion of the external skin, which in the development of the embryo becomes pushed in to form a hollow bladder; the bladder or sac becomes complicated, and the tube by which it originally opened to the surface

becomes much narrowed or entirely closed. In Elasmobranchs this tube has a small opening on the surface of the skull throughout life, but in other fishes it is closed in the adult. There is no middle or external ear in fishes, for the middle ear or tympanum is represented by the spiracle and no external ear is formed. The auditory sac contains calcareous matter secreted by its wall and known as otoliths; the function of these is to convert the sound vibrations into movements of solid matter which have more effect in stimulating the terminations of the auditory nerve. In the dog-fish the calcareous particles are small and separate, in the bony fish they are consolidated into large concretions which increase in size during growth by the addition of layers to the exterior; the deposits of successive years can often be distinguished, and in this way the age of the fish when it was killed can be ascertained.

The skin may be supposed to possess the sense of touch all over its surface as a result of the presence of terminations of sensory nerves, without any special organs, but there are also definite sense-organs in the epidermis composed of groups of sensory cells united into spindle-shaped bodies called end-buds; these are irregularly distributed over the body, on the fins and lips, and also in the epithelium of the mouth and pharynx. In this latter position they form the organs of the sense of taste. But the most peculiar and special sense-organs of fishes are the sense-organs of the lateral line. These are somewhat similar in structure to those already mentioned, but they are usually sunk beneath the surface and contained in tubes, grooves, or closed canals; in all cases they are developed on the surface of the epidermis and afterwards enclosed in invaginations. The most constant part of this system is the lateral line, which is a tube in the skin extending from the auditory region along each side of the body to the root of the tail. In the dog-fish, as in most Teleosts, this tube is closed and communicates with the surface of the epidermis by pores at regular intervals; it has thus a structure very similar to that of a tube-railway, the pores corresponding to the stations at which the tubular tunnel communicates by vertical shafts with the surface of the ground. The sense-organs are in the epithelium lining the tube, on its inner surface, alternating with the pores; in Teleosts the tube perforates a series of modified scales which make a conspicuous

line on the side of the fish. The sense-organs are innervated by a branch of the tenth cranial nerve called the vagus, this branch running parallel to the tube and sending a small branch to each sense-organ. On the head the structures of this system are not so constant: in Teleosteans they form tubes like that of the lateral line, one running above the eye, another below the eye and along the upper jaw, and a third along the front of the operculum and the lower jaw; these tubes are all supplied by branches of the seventh cranial nerve. In the dog-fish, on the other hand, and in most Elasmobranchs, the tubes on the head are represented by separate tubes each opening by a pore and running obliquely beneath the surface of the skin; these sensory tubes are situated in the same regions as the continuous tubes of Teleosts, and are supplied by the same nerves. It will be noted that the series of lateral-line organs radiate from a focus formed by the auditory organ which is really to be regarded as a special and enlarged sense-organ of the same system.

The primary reproductive organs or gonads are outgrowths of the epithelium lining the body cavity. In Elasmobranchs the ovary has no connection with the oviducts; the eggs, as in the majority of vertebrates, are set free in the body cavity and make their way into the open internal ends of the ducts; the latter are provided in the oviparous species with glands which secrete a flexible, tough egg-shell of oblong shape. In the male the testes are connected by fine efferent ducts with the epididymis, originally a part of the kidney system, while the functional kidney situated behind the epididymis has ducts of its own. In the bony fishes the original oviducts degenerate and become shorter and in the most modified Teleostei, such as the Perch or Cod, the mouth of the duct has become continuous with a sac which encloses the ovary so that the eggs do not become free in the body cavity; in the bony fishes also there is no shell-gland and therefore no egg-shell, and the eggs when shed are enclosed only in the vitelline membrane formed in the ovary. In the male bony fishes the efferent ducts of the testis have become a single duct which has separated from the urinary duct and opens directly to the exterior. In the Elasmobranchs the intestine, the generative ducts, and the urinary ducts all open into a common sac, the cloaca, which has a single opening to the exterior as in birds and reptiles; in the

Teleosteans, on the other hand, the anus, generative opening, and renal opening are separate on the ventral surface in the order mentioned.

In accordance with the various degrees of structural difference, some of the most important of which have been mentioned in the above general survey, the class of fishes can be divided and subdivided in a systematic classification, as shown in the following table :—

Sub-Class.	Order.	Sub-Order.	Families.
Elasmobranchii.	Plagiostomi.	Selachii.	Notodanidæ. Chlamydoselachidæ. Heterodontidæ. Scylliidæ. Carchariidæ. Sphyrinidæ (Hammer-heads). Lamnidæ. Cetorhinidæ. Spinacidæ. Pristiophoridæ.
		Batoidei.	Pristidæ, Saw-fishes. Rhinobatidæ. Raiidæ, Skates and Rays. Torpedinidæ, Torpedos. Trygonidæ, Sting-rays. Myliobatidæ, Eagle-rays.
Holocephali.			Chimæridæ.
Dipnoi.			Ceratodontidæ. Lepidosirenidæ.
Teleostomi.	Crossopterygii (Fringe-fin- ned Gan- oids).		Polypteridæ.
	Chondrostei (Cartilagin- ous Ganoids).		Polyodontidæ } Sturgeons. Acipenseridæ }
	Holostei (Bony Ganoids).		Amiidæ, Bow-fin. Lepidosteidæ, Bony-pikes.
	Teleostei.	Malacopterygii (Soft-finned).	Elopidæ. Albulidæ. Mormyridæ. Hyodontidæ. Notopteridæ. Clupeidæ (Herrings). Salmonidæ (Salmon, etc.). Alepocephalidæ. Stomiatiidæ, etc.

SUB-CLASS.	ORDER.	SUB-ORDER.	FAMILIES.
		Ostariophysi (Bladder connected with ear).	Characiniidæ. Gymnotiidæ. Cyprinidæ (Carps). Siluridæ (Cat-fishes). Loricariidæ. Aspredinidæ.
		Symbranchii (Gill-openings united).	Symbranchidæ. Amphipnoidæ.
		Apodes (Without pelvic fins).	Anguillidæ (Eels). Murænidæ. Saccopharyngidæ, etc.
		Haplomi (Simple shoulder-girdle).	Esocidæ (Pikes). Galaxiidæ. Haplochitonidæ. Scopelidæ. Cyprinodontidæ. Amblyopsidæ, etc.
		Heteromi (Abnormal shoulder-girdle)	Fierasferidæ. Halosauridæ, etc. Gastrosteidæ (Sticklebacks).
		Catostomi.	Syngnathidæ (Pipe-fishes). Pegasidæ (Sea-horses). Lampridæ. Solenostomidæ, etc.
		Percesoces (Perch-pikes).	Mugilidæ (Grey mullets). Scombresocidæ (Gar-fish, etc.). Atherinidæ (Sand-smelts). Ammodytidæ (Sand-eels). Stromateidæ. Sphyrænidæ. Anabantidæ (Climbing Perches), etc.
		Anacanthini (Without spines).	Gadidæ (Cod, Haddock, Whiting, etc.). Macruridae. Marænolepididæ.
		Acanthopterygii (Spiny-finned).	Div. 1. Perciformes (Perches, etc.). ,, 2. Scombriformes (Mackerel, e.c.). ,, 3. Zeorhombiformes (Flat-fishes and John Dory). ,, 4. Kurtiformes. ,, 5. Gobiiformes.

Sub-Class.	Order.	Sub-Order.	Families.
		Acanthopterygii (Spiny-finned)— <i>continued.</i>	6. Discocephali (Sucking fish). " 7. Trigliformes (Gurnards). " 8. Blenniiformes (Blennies). " 9. Trachypteriformes (Rubber-fishes). " 10. Mastacembeliformes.
		Pediculati.	Lophiidæ (Anglers). Ceratiidæ. Antennariidæ. Malthidæ.
		Plectognathi (Jaw-bones united).	Triacanthidæ (Trigger-fishes). Triodontidæ. Balistidæ (File-fishes). Ostraciontidæ (Cow-fishes). Tetrodontidæ } Diodontidæ } Molidae (Sun-fishes).

## CHAPTER II

### EVOLUTION AND PALÆONTOLOGY

The extinct Ostracoderms. Fossil Elasmobranchs. Crossopterygians and Dipnoi evolved in fresh water. Pedigree of Teleostomi. Relative abundance of different orders in past and present times.

In a general way it is evident from the preceding summary of structure and classification that the shark-like fishes or Elasmobranchs are the most primitive of existing fishes, and that the bony fishes can be derived from these by modifications of the various organs; also that the Ganoids are the more primitive of the bony fishes, and the Teleostei the most modified. Among the Ganoids, the "fringe-finned" forms or Crossopterygii are the most primitive, being nearest to the Elasmobranchs in the structure of the paired fins. The Dipnoi, or lung-fishes, on the other hand, might be supposed to be the latest stage in the evolution of fishes, especially on account of the advanced stage of evolution shown by the lungs in adaptation to atmospheric respiration; but on the other hand in structure the Dipnoi show unmistakable affinities to the Crossopterygii. In order, however, to discuss the evolution of fishes we must consider the evidence afforded by the chronological succession of fossil forms as well as the evidence of the structure of existing forms; we must study palæontology as well as comparative anatomy, and include under the latter term the study of development or embryology. We will proceed therefore to give a brief outline of the most important facts concerning the palæontology of fishes.

There is no evidence of the derivation of fishes with jaws from those with suctorial mouths (Cyclostomes) resembling the lampreys and hags. Minute fossils known as Conodonts occur in the most ancient stratified rocks called by geologists palæozoic, from the Lower Silurian to the Carboniferous Lime-

stone, and have been compared to the teeth of the Cyclostomes ; but these fossils in microscopic structure do not resemble such teeth, and nothing can be said about them. Small fossils about two inches long found by Dr. Traquair in the Caithness flag-stones near Thurso appear to have the structure of Cyclostomes, but they have a calcified internal skeleton, while the skeleton of existing Cyclostomes is soft and cartilaginous.

The ancient fossils called Ostracoderms are believed to resemble the lampreys in the absence of jaws and paired fins. These are certainly the oldest known remains of vertebrates, but unfortunately it is impossible to connect them with any of the ordinary types of fishes. Their structure is quite peculiar, and no transitional forms are known leading to sharks or other fishes. The name means shell-skinned animals, and refers to the calcified plates which cover the body, or at least the head. The head region was covered with a large single dorsal plate, in *Pteraspis* there was a ventral plate also. The under region of the body was covered with series of bony scales somewhat like those of a Ganoid. In *Pterichthys* there is a pair of jointed limbs at the sides of the head, but these do not correspond to pectoral fins, they are merely the lateral angles of the head-shield produced and jointed. Unpaired fins are, however, present, but they are formed entirely by parts of the dermal scales. There is a dorsal fin, an asymmetrical (heterocercal) tail fin, and sometimes a ventral fin. These in structure correspond to the dermal part of the fins of fishes : but there is no trace of internal skeleton. The character of the armour, and the grooving of the armour-plates for sensory canals indicate that the animals were fishes, and Smith Woodward finds indications of gill-pouches. The Ostracoderms have been found only in the Upper Silurian and the Devonian rocks. In 1859 a specimen of *Pteraspis* was found in the Lower Ludlow beds in Shropshire, belonging to the Silurian. This fossil was associated with marine shells, especially Cephalopoda or cuttle-fishes, so that it might be concluded that the fish was marine. *Pteraspis* also occurs in the bone-bed of the Upper Ludlow formation near Ludlow, in which the greater part of the fish remains belong to the Elasmobranchs. This also indicates a marine habitat. Of the English Devonian strata, the beds which occur in Devon are of marine character, while those of Scotland, to which the name

Old Red Sandstone was originally given, have many fresh-water characteristics. It does not follow, however, that all the formations were fresh water. *Pteraspis* and *Cephalaspis* occur in the Lower Old Red in Perthshire; considering that no shells or corals have ever been found in the Old Red Sandstone of Scotland, it would seem from this evidence that the Ostracoderms were fluviatile. They may of course have lived also on the sea-coast, or if estuarine their bodies may have been sometimes carried down to the sea and this may be the explanation of their occurrence in the marine deposits mentioned above. Higher than the Devonian they do not occur, and we have no evidence that any more recent forms are descended from them. They appear to have become extinct, leaving no descendants.

With regard to the other principal types of fishes, we may postpone the special consideration of the Teleosteans, which we know to have arisen by gradual transformation of the original Ganoids in the Cretaceous period, but of the four chief divisions of the fishes proper, those provided with jaws, namely Sharks, Chimæroids, Lung-fishes, and Teleostomes, we find that all were in evidence contemporaneously in the earliest period of which we have any record. All occurred in the Devonian. Thus there is only a single group of importance which has been evolved since the beginning of the geological record, namely the Teleostei. During the same time all the widely divergent types which inhabit the land have arisen, Amphibia from Dipnoans, Reptiles from Amphibia, and Birds and Mammals from Reptiles. Evolution is thus the history of the invasion of new media: the watery medium was already occupied at the beginning; amphibia partly, reptiles entirely acquired the power of living on dry land, flying reptiles invaded the air, and that sphere was afterwards more fully occupied by the birds, while the mammals again, having like the birds become independent of external variations of temperature made a more complete conquest of the land.

That fishes of the shark type existed in the Upper Silurian is proved by the so-called ichthydorulites, or fish-spines of the Upper Ludlow bed.

Similar spines of Elasmobranchs occur in the Lower Old Red Sandstone of Scotland; but few complete skeletons or remains showing the shape and character of the entire fish

have been discovered in beds of this age. *Climatius* is an interesting exception. This fish occurs in the rocks of Forfarshire. It belongs to the group of extinct Elasmobranchs called Acanthodians, from the fact that there is a strong, straight spine in the anterior margin of each fin, paired and unpaired. There is a peculiarity in this fossil which occurs in no other fish, namely, that instead of two pairs of lateral fins, there are on each side of the ventral region a series of fin-spines, apparently five in number, and this case affords the strongest support to the theory that the original condition was a pair of continuous lateral fin-folds, of which the pectoral and pelvic fins are the remaining portions.

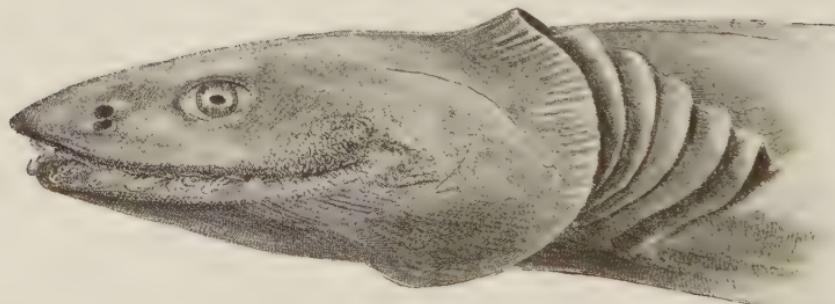
It may appear that the occurrence of *Climatius*, an Elasmobranch fish, in the Lower Old Red Sandstone is inconsistent with the conclusion drawn above, that the other fishes found in this formation were inhabitants of fresh water, and with the general view of fish-evolution adopted by the present writer. But geologists tell us that the Lower Old Red shows a transition from marine to lacustrine conditions, and on the other hand the Acanthodians themselves may possibly have been fresh-water or estuarine fishes. They show in some of their characters approximations to the condition of the earliest Ganoids, namely the terminal mouth, flattened and enlarged dermal plates with enamelled surfaces, and the partial development of a gill-cover. We have no evidence, however, that the Acanthodians were actually ancestral to the bony fishes.

In the Carboniferous and Permian strata some remarkable forms of the shark type have been obtained in recent years in a very well-preserved condition. The most primitive and earliest of these is *Cladoselache*, found in Lower Carboniferous strata in Ohio. Its mouth is at the end of the snout. It is from two to six feet long. The paired fins are attached horizontally by a wide base, and have the appearance of enlarged portions of an originally continuous fold. The tail is short and high vertically, with an extremely heterocercal structure; that is to say, the termination of the trunk is bent upwards almost at right angles and the ventral fin-rays are very long. The Acanthodians already mentioned extend from the Silurian to the end of the Permian and therefore go back to an earlier period than *Cladoselache*; but Professor Bashford Dean con-





HAMMER-HEADED SHARK



HEAD OF *CHLAMYDOSELACHUS ANGUINEUS*, AFTER GARMAN,  
SHOWING THE SIX GILL-SLITS



*CHIMAERA COLLIEI*, AFTER BASHFORD DEAN

siders nevertheless that the latter represents the ancestral form of the Acanthodians.

*Pleuracanthus*, which occurs in the Carboniferous and Permian both in Europe and North America, on the other hand, differs in many respects from sharks, and in these same features approximates to the Dipnoi. It was a shark in the following features: the gill-slits opened separately on the surface; the jaws consisted of the same primitive cartilages as in sharks, claspers occurred in the male. On the other hand, the paired fins show a transition to the feather-like or pinnate structure which is in reality not primitive but secondary, the basal cartilages being separated from the body at the posterior end, and the radial cartilages extending round to the posterior, originally the internal, side, so that a structure is produced which has a central axis and rays along each side. But the feature most similar to the lung-fish was that the dermal denticles had disappeared from the skin of the trunk, and on the head had developed into dermal bones arranged like those of the lung-fish. The tail retained the primitive symmetry and was not of the heterocercal or shark type.

*Pleuracanthus*, therefore, looks like the ancestor of the lung-fishes, and seems to show how these were derived from the shark type.

True Dipnoi, however, are found in strata much older than *Pleuracanthus*, and we can only suppose that the latter type may have been in existence earlier than the Dipnoan, though not preserved or not yet discovered.

It might be expected, since the shark type is assumed to be the earliest, that forms like the existing sharks and dog-fishes would occur among the fossils of the oldest rocks, whereas the examples we have mentioned are in many important characters different from existing species of the group. The answer to this is that the cartilaginous skeleton, would be likely to putrefy before being imbedded in sediment, and that large numbers of spines and teeth certainly belonging to fishes of the group are preserved. Again it is only maintained that the *type* was the earliest, not necessarily that all the existing forms have come down from the earliest times unchanged. Of existing forms *Chlamydoselachus* (Plate XXI., B) which occurs in about 150 fathoms off the coast of Japan, off Madeira and off Norway and

of which the head region is figured seems to show most resemblance to Palæozoic sharks. It has six gill-slits, the mouth is terminal and the teeth three-pronged.

Forms allied to the Port Jackson shark, *Cestracion*, have been recognised in the Carboniferous formations, and *Cestracion* itself from the middle of the Secondary period onwards. Members of the *Scyllium* family, to which the common spotted dog-fishes belong, in the middle of the secondary period, and in the Cretaceous or Chalk period occurs the spiny dog-fish (*Acanthias*). The latest sharks to appear are the great man-eating species of *Carcharias* and their nearest allies, remains of which have only been recognised in the Tertiary formations.

Assuming that the ancestral fishes were Elasmobranchs, as we are bound to do from the fact that the flat bones of the head and of the pectoral girdle of bony fishes are derived from the dermal denticles of the Elasmobranch, the earliest bony fishes must have had a Crossopterygian or fringed structure in their lateral fins. From the Crossopterygian fringe-finned type was derived the ray-finned type by the reduction of the internal radials, and the lung-fish (Dipnoan) in another direction by the development of an elongated axis to form the biserial or pinnate type of fin. The Crossopterygian is therefore a central type, and its fossil forms should be among the oldest. This is, in fact, the case but they are not found among the fossils at present known to distinctly precede the Dipnii; examples of both groups occur in the Devonian age, most of them having been obtained from the Old Red Sandstone of Scotland. The earliest of these two types are much more similar to each other than the later representatives, as is easily seen by comparing the Crossopterygian *Osteolepis* with the Dipnoan *Dipterus* both from the Old Red Sandstone. The chief difference between them is the presence of well-developed teeth on the dermal jaw-bones of the former, their absence in the latter. The edge of the upper jaw in *Dipterus* is, however, calcified and bony, although distinct maxillæ and premaxillæ cannot be recognised, and in this and other respects the existing Dipnii are not primitive but degenerate or modified. In both forms the tail is heterocercal, and there are two dorsal fins and one ventral. With regard to the scales, those of *Osteolepis* are of the Ganoid type, rhomboidal and enamelled, those

of *Dipterus* thick and enamelled but cycloid and overlapping. In other Crossopterygians, the scales are cycloid and the resemblance is still greater as is evident from Fig. 23, A and B. *Holoptychius flemingi* represented in A occurs in the Upper Old Red Sandstone.

There is good reason, as we have seen above, to believe that the Old Red Sandstone is a fresh-water formation and that these fishes, therefore, lived in fresh water. From the fact that existing Crossopterygians and Dipnoi live in fresh water and have respiratory air-bladders or lungs we may conclude that this was the original function of the air-bladder, and that both

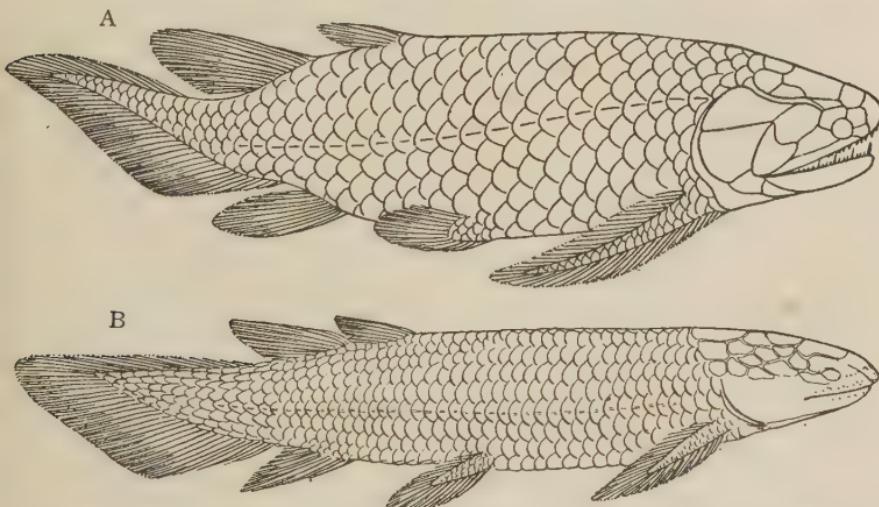


FIG. 23.—A, *Holoptychius flemingi* from Upper Old Red Sandstone; B, *Dipterus valenciennesi* from Middle Old Red Sandstone.

the air-bladder and the change in the dermal skeleton arose in consequence of the change from a marine to a fresh-water habitat. We cannot give a reason for a change in the dermal skeleton, but in the case of the air-bladder there need be little doubt that it arose in fishes originally of the Elasmobranch type which had ascended from the sea into rivers or swamps where in consequence of a warm climate and rotting vegetation there was a deficiency of oxygen in the water and the fish acquired the habit of taking air into the gullet. The difference between the two types of these ancestral air-breathing fishes, the Crossopterygian and the Dipnoan, was evidently chiefly due to the difference in mode of feeding, the Dipnoan having tooth-plates adapted to crushing and masticating hard or vegetable food,

while the Crossopterygian was predatory and developed the teeth on the external dermal jaw-bones. A further step in the direction of air-breathing habits led to the Amphibia, but we cannot derive these directly from the Dipnoan because they have well-developed tooth-bearing maxillæ and premaxillæ, while on the other hand they differ from the Crossopterygian in having the upper jaw fixed directly to the skull. It is best to conclude that the three types, Crossopterygian, Dipnoan, and Amphibian, arose by divergence from the original Elasmobranch fishes which came from the sea to the fresh waters of the Palæozoic period. The existing Dipnoans have degenerated in the structure of limbs and tail; the heterocercal tail is adapted to vigorous motion and to the habit of feeding from the ground or of plunging into the depths, for the lower lobe of the tail being most developed throws the tail upwards and the head downwards. The Dipnoi living in narrow waters are sluggish in habit and consequently the tail fin has degenerated and a secondary symmetrical tail has been formed from dorsal and ventral fin-rays, the paired fins are mostly slender and rudimentary, and the body has become elongated and eel-like. In the Secondary or Mesozoic period the Dipnoi appear to have been represented by *Ceratodus* or a form very slightly different, and the only remains of these fish which have been preserved are the dental plates or the parts of the skull; these have been found in almost all parts of the world.

We cannot trace a complete series of intermediate stages from the palæozoic Crossopterygians to the existing forms of the same type, namely the African *Polypterus* and *Calamoichthys*. *Polypterus* has rhombic ganoid scales like those of the Devonian *Osteolepis*; unfortunately no fossil Crossopterygians are known from Tertiary formation, and those of the Secondary period called Cœlacanthidæ are less primitive in their scales and other structures than *Polypterus*; the scales of Cœlacanthidæ are cycloid, the terminal part of the tail is disappearing and the basals of the two dorsal and single ventral fins are united into a single, forked bone. From the Crossopterygians are derived the ray-finned fishes (Actinopterygians), in which the lungs gradually lose their respiratory function and paired character, and become more and more completely adapted to serve as an air-bladder which diminishes the specific

gravity of the fish. In the evolution of these forms we can trace a gradual return to the sea, for among existing fishes the more primitive forms live more or less completely in fresh water, and the most recent and most modified are typically marine. The fins of Actinopterygians are characterised by the reduction of the basal lobe and its internal skeleton, the dermal rays arising from the surface of the body. The oldest form is *Chirolepis* which occurs in the Lower Old Red Sandstone together with the earliest Crossopterygians. This genus belongs to the group or branch of the Chondrostei and is the first of the great family Palæoniscidæ which developed an abundance of species and individuals in the Carboniferous and Permian formations and gradually diminished in the Secondary period till the end of the Jurassic. These fishes had a complete armour of ganoid scales, a large heterocercal tail, and a single dorsal fin in the middle of the back. The dermal bones of the head were external and were simply the ganoid plates of that region. As the Palæoniscidæ are disappearing the family Chondrosteidæ comes into existence, distinguished by the degeneration of the scales on the body; specimens occur in the Lias or Lower Jurassic, and these forms must be regarded as directly descended from the Palæoniscidæ. The Chondrosteidæ, on the other hand, are the ancestors of the existing Sturgeons, which are not known before the Tertiary. A branch from the Palæoniscidæ gave rise to the Platysomidæ which existed in the Carboniferous and Permian periods; they are deep-bodied compressed fishes completely covered with ganoid scales, but with short jaws carrying blunt crushing teeth; they do not appear to have given rise to any later forms.

The Holostei seem to have been derived from the Palæoniscidæ through the Catopteridæ which are small fishes found in the Triassic rocks of North America, Europe, and Australia; they have the ganoid scaling, but the dermal fin-rays of the median fins are almost reduced to the number of the supporting radials as in the Holostei, and the upper lobe of the tail is diminished, so that the homocercal condition is approached. The Holostei are a large and diversified group which include forms that are transitional to the more primitive Teleostei. The more primitive and earlier forms retain the ganoid scaling, while some of the later have cycloid scales and perfectly homo-

cercal tails. They first appear in the Permian, but were only abundant in the Trias and still more so in the Jurassic, while in the Cretaceous the Teleostei become the dominant type. The family Eugnathidae, fishes much like a tarpon or large herring in shape and fins, appear first in the Trias and are common in the Jurassic; some of them have the ganoid scaling, while in others the scales are thin, cycloid, and overlapping. The American Bow-fin, *Amia*, is a surviving member of this group, retaining the incomplete vertebræ in the tail, and a bony plate under the throat, which are primitive features. *Caturus* and *Eurycormus* of the Jurassic lead directly to the soft-finned Teleostei (Malacopterygii) such as Tarpons (Elopidae) and Herrings (Clupeidae). The latter family were already abundant in Cretaceous times and are sometimes fossilised in dense shoals. The Pycnodonts, deep-bodied ganoids with crushing teeth, seem to have became extinct in the Lower Eocene without leaving any descendants. *Lepidosteus*, the bony Pike of North America (Plate XX., C), is a pike-like, predaceous modification of the earlier Holostei, but in the fossil condition it is only known as far back as the Eocene, when it lived in Europe as well as in America.

The ancestry of the several divisions of Teleostei has not yet been worked out, but it is probable that they have descended separately from the fossil ganoids, and not all from the most primitive Malacopterygii above mentioned. It has been suggested that the Cat-fishes (Siluridae) were descended directly from the Chondrostei, and are therefore more allied to the Sturgeons than to the Malacopterygii, but it is a question whether the equality of dermal rays and radials could have been evolved twice independently. There seems greater probability that the cod-like fishes (Anacanthini) may have been derived directly from the extinct Cœlacanthidæ; although the latter are placed among the Crossopterygians it is remarkable that the dermal rays both dorsal and ventral at the posterior end of the body are equal in number to the internal radials as in the Teleostei. The original termination of the tail is disappearing, and the dorsal and ventral rays are symmetrical as in the cod family (Gadidae). The chief difficulty in the hypothesis is that in the Cœlacanthidæ there are two short dorsal fins and one ventral whose basals are fused into a single bone,

but it seems not impossible that these fins might have disappeared altogether and the posterior rays have extended forwards. With regard to the anterior position of the pelvic fins in the Gadidæ it is to be remembered that they are not directly attached to the pectoral girdle, while in the Cœlacanthidæ these fins show a marked approximation to the pectorals. The lobes at the bases of the paired fins are much reduced in Cœlacanthidæ as compared with other fringe-finned ganoids. Cœlacanthidæ, e.g., *Macropoma*, extend to the Cretaceous, and fossil forms of Gadidæ begin to appear in the following period, the Eocene.

The most primitive of the spiny-finned Teleosteans (Acanthopterygii) are also the most ancient of the fossil forms belonging to this Order, namely the Berycidæ, which were already abundant in the Chalk period. They are closely similar to the ganoid Eugnathidæ in most of their characters, only differing in the presence of a few spines in the dorsal and ventral fins and the attachment of the pelvic bones to the pectoral girdle. In *Beryx* and *Holocentrum* the air-bladder even retains its communication with the digestive tube. There can be little doubt that these early examples of the spiny-finned type were evolved in the sea, and that the comparatively few existing fresh-water forms, such as the Perch, have ascended from the sea at some later period.

The above may seem a somewhat technical and condensed discussion, beyond the easy comprehension of the average reader. It is however impossible to state the most important facts concerning fossil fishes, and the relative age of the geological strata in which they occur, without the use of some technical terms. We will endeavour to give in simple language the chief conclusions which our present knowledge enables us to draw concerning the evolution of fishes. In the broadest sense it may be said that there are two principal types of structure in fishes, the shark type and the bony type. At the present time fishes of these two types exist in large numbers and in great variety side by side in the sea. We cannot maintain that the differences of structure between sharks and bony fishes correspond to equally marked differences in mode of life: the shark and the tunny are both voracious monsters living as far as we can see much in the same way, both

powerful swimmers, both feeding on other fishes, both ranging through the surface waters of the open ocean. We cannot perceive that the bony fish was derived from the shark-like fish by adaptation to a different mode of life in the sea, as the Amphibian was derived from the fish by adaptation to a life on dry land in its adult condition. What then is the explanation offered by the doctrine of evolution for the existence of these two types?

When we turn to the study of fossil fishes, we find that in the most ancient stratified rocks both types were represented, but the fossil forms of the bony type, belonged exclusively to certain groups of which at the present time very few species exist, and these only in fresh water, namely the Fringe-finned Ganoids, represented now by the African *Polypterus*, and the Lung-fishes which occur now in tropical rivers or swamps. Both these kinds of fishes have lungs, or open air-bladders actually used for breathing air. The Lung-fishes evidently resemble the ancestors of the Amphibia, while from the Fringe-finned Ganoids we have a series of diverging forms leading to the great variety of existing bony fishes. The conclusion is that the bony fishes of the sea at the present day are descended from fresh-water fishes of ancient times, which were adapted to breathe air in order to supplement the original respiration by gills. In this way we can understand the origin of the air-bladder, which is wanting in the shark type. The air- or gas-bladder is evolved from lungs, not lungs from air-bladder. At the same time the skeletal structures both within the body and in the skin underwent a change to the bony type with the change of habitat from the sea to fresh water. From the Fringe-finned Ganoids descended numerous diverging forms which populated the various fresh waters of the globe, and ultimately reached the sea again and established themselves there along with the fishes of the shark type. The first important change in the transition from the fringe-finned type to the modern fishes was the reduction of the internal skeleton of the paired fins, so that the basal fleshy lobe disappeared and the fin became fan-like. It is difficult to say with certainty, which of the extinct fan-finned Ganoids were first to reach the sea: it is probable enough that many of the groups lived along the sea-coast, but we know that, excepting the Sturgeons, the only sur-

viving forms, *Lepidosteus* and *Amia* of N. America, live in fresh water, and the sea is inhabited by the latest results of evolution in fishes, the Teleostei, together with Elasmobranchs or fishes of the shark type.

In numbers of individuals certainly, and probably in the number of species also, fishes at the present time are superior to all other classes of vertebrates, and this is not to be wondered at when we remember that the sea covers about three-fourths of the surface of the globe and that the waters of the land also teem with fishes. Birds are able to range over the ocean as well as over the land, but they are dependent on the land for breeding. At present about 12,000 species of fish are known and of these about 11,500 belong to the order of Teleosteans. The next most abundant order is that of the Elasmobranchs. The Holocephali or Chimæroids are few in number and confined to the deeper parts of the sea ; of Dipnoi Fringe-finned, and Bony Ganoids there are only a few surviving species, and the Sturgeons are not much more numerous, although some single species among the last two groups are abundant in individuals, for example *Lepidosteus* and *Acipenser* in North America. In former periods of the earth's history the proportions were very different : Teleostei began their domination in the Cretaceous period, in the Jurassic or middle of the Secondary period the Holostei were the most abundant, in the Trias and Carboniferous rocks remains of Chondrostei are most numerous together with Crossopterygians and Elasmobranchs. Crossopterygians and Dipnoi are characteristic of the Carboniferous and Devonian, while the Elasmobranchs, which occur in all formations extend back to Silurian times, where they are accompanied by the strange forms called Ostracoderms, whose relation to the fishes is as we have seen quite problematical. Fishes are dependent on nothing but water and food, and wherever there is water there are fish, some species being able to live at least temporarily even where there is no water, as the eel and the tropical fishes provided with organs for atmospheric respiration, such as the climbing perch (*Anabas*) and the lung-fishes (*Dipnoi*). The abundance of some species where they have not been diminished by human agency, either in direct destruction or by pollution of the waters, is very great, and can only be compared to that of some kinds of insects. Some years ago Guillemard described

the multitudes of Salmonidæ which ascended the rivers of Kamtchatka in the spawning season as so great that the banks were covered for miles with heaps of dead and dying fish, which were crowded out of the water or were exhausted by the process of spawning. When the tile-fish was destroyed by some change of current off the east coast of the United States it was estimated that about 1,500,000,000 of the dead fish floated at the surface of the sea. Probably the most abundant of all fishes are the herrings in the North Atlantic and other species of Clupea in the North Pacific; in the year 1907 over 6,000,000 cwts. of herrings were landed in Scotland alone. The weight of a single herring is from four to eight ounces; if we take an average of three to a pound the above total weight would represent about 2,016,000,000 herrings. The total number captured annually in the North Atlantic has been estimated to be 3,000,000,000, and this is probably not a very large percentage of the number in existence at a given time. Cod also occur in millions off the shores of Norway and Newfoundland, and even among Elasmobranchs the spiny dog-fish (*Acanthias*) occurs sometimes in vast shoals which make drift-net fishing impossible.

## CHAPTER III

### DISTRIBUTION AND LOCATION

Fresh-water fishes and marine fishes. Physostomous fishes originally belonging to fresh water, and Acanthopterygians which have returned thither from the sea. Fresh-water fish-fauna of the great continents. Natural homes and habits in littoral zone. Tropical fishes. Arctic and Antarctic fishes. America and Europe. North Pacific. South Africa. India. New Zealand and Australia. Pelagic fishes. Abyssal fishes.

**I**N considering the waters of the earth as the habitat of fishes, the first distinction that we naturally make is between the fresh waters and the sea. The conditions in the former are necessarily different from those in the latter, although there are regions of transition between the two. In the rivers space is more limited, light is abundant, the vegetation and animal life are quite different from those in the sea, but the chief difference is the absence of salt from the water. In some cases communication with the sea is difficult or impossible, but even where it exists many species do not migrate and cannot live in salt water. Temperature limits the range of some species, those which are natives of the tropics could not survive in colder regions, but the fact that fish of various species thrive and multiply when introduced to distant regions of similar climate where they do not naturally occur, shows that their natural range is determined not merely by suitable conditions, but by physical barriers to dispersal. As we have seen in considering the evolution of fishes, the Elasmobranchs are almost entirely marine, only a few of the flattened forms, belonging to the Sub-Order Batoidei, entering large rivers in the tropics, and a few becoming land-locked: Indian species of saw-fishes, *Pristis*, thus enter rivers, and one in the Gulf of Mexico ascends the lower Mississippi. Some species of *Trygon* or sting-rays are confined to fresh water in the northern part of South America. Nearly all the surviving primitive bony fishes, on

the other hand, are entirely confined to fresh water, namely, the Dipnoi, the Crossopterygians, *Polypterus* and *Calamoichthys*, and the Holostei, *Lepidosteus* and *Amia*. The Chondrostei or sturgeons also live in rivers, with the single exception of *Acipenser*, some species of which descend to the coasts to feed.

Among the fishes of the familiar scaled and bony type included in the order Teleostei the majority of the families in the five most primitive Sub-Orders, possessing open air-bladders, are inhabitants of fresh water. All the families of the carps and their allies (Ostariophysi) are confined to fresh water except three genera of the Siluridæ or cat-fishes which are found along the coasts and in estuaries. Of the Malacopterygii, to which salmon and herring belong, the majority of the families, but not all, are entirely confined to fresh water, namely the Mormyridæ of Africa, with ten genera, the Hyodontidæ, containing only a single genus found in North America, the Notopteridæ, with two genera in Africa and southern Asia, the Osteoglossidæ, with four genera in the tropics, the Pantodontidæ, including only the little *Pantodon buchholzii* of West Africa, the Phylactolæmidæ, also consisting of one species living in the Nile and Congo, and the Cromeriidæ, with a single genus of fishes occurring in the white Nile. The Salmonidæ range from fresh water to depths of 2000 fathoms in the ocean, and some of the species, like the salmon, migrate from sea to fresh water and back again; we cannot say why the marine species have not developed spines like the majority of marine Teleosts, but some of them have lost the air-bladder altogether. Of the Clupeidæ (herring family) few species are confined to fresh water, but several like the shads of Europe and North America ascend rivers for the purpose of spawning. The Symbranchii live in fresh water, while the Apodes or true eels, like the Salmonidæ, range from rivers to the deep sea. Among the Haplomi there are several families characteristic of the fresh-water fauna, such as the Esocidæ or pikes, the Cyprinodonts or toothed carps, of which a few species live along the sea-coasts, the Haplochitonidæ of the southern hemisphere, and the Percopsidæ; some of the Galaxiidæ go down to the sea to spawn. The Catostomoi or stickleback group as a whole are marine, but several species of sticklebacks are common in fresh waters. The Percesoces (e.g. flying fishes)

are also marine, but the three families of the Labyrinthici, the serpent-heads, climbing perches, and gouramis, are adapted to live exclusively in fresh water. These last must be regarded, like the fresh-water Acanthopterygii (spine-finned fishes), as fishes which have returned from the sea to inland waters. Of fresh-water Acanthopterygii the most characteristic are the Percidæ (perches) of the northern hemisphere, evidently related to the Serranidæ, justly called sea-perches. The Centrarchidæ or sun-fishes of North America are another fresh-water family allied to the perches. There can be no doubt that the Cichlidæ of the tropics are derived from Labridæ (wrasses) which have ascended from the sea. In cases where a single species of a family, as the miller's thumb among the bull-heads (Cottidæ) and the burbot among the cod-family (Gadidæ), lives in fresh water, it is obvious that it is recently derived from marine ancestors. Lastly fresh-water forms include the Mastacembelidæ, placed in a separate Sub-Order, and a few species of Plectognathi; these also have been secondarily adapted to their present habitat.

The distinguishing features of the fresh-water fish-fauna of the great continents may here be mentioned. (See Map, Plate XXII.) In Europe and northern Asia there are no lung-fishes (Dipnoi) and of the ganoid forms only the sturgeons (Chondrostei) are represented; of these the true sturgeons are abundant in Europe. *Acipenser sturio*, the common sturgeon (Plate XX., B) is frequently caught in the North Sea and occurs also in the Mediterranean, ascending all the great rivers; the great Russian sturgeon, *A. huso*, is common in the Volga and the little sterlet inhabits the Danube and other rivers flowing into the Black Sea and Caspian. Of the soft-finned fishes (Malacoptyergii) the characteristic families are the carps (Cyprinidæ) and Salmonidæ; among the former the loaches are almost confined to this region, and of other members of the carp family there are numerous species which are abundant in individuals such as our roach, dace, chub, bream, etc. Of Salmonidæ we have the trout, salmon, and numerous species of char and white-fish or *Coregonus*. Siluridæ or cat-fishes, are almost entirely absent, the few species which occur being immigrants from India or North America; in Europe there is only one species, *Silurus glanis*, the wels, which lives in the

Danube; in Asia are found *Macrones* and *Pseudobagrus* which are more common in India, while in China occurs one species of the North American genus *Amiurus*. The Esocidae or pike family are characteristic of the region we are considering, although there are only two species, the pike and a small fish called *Umbra crameri*, living in stagnant waters in Austria and Hungary. Of Percidae there are several species, the common perch, widely distributed, the pope, *Acerina cernua*, the large pike-perches, *Lucioperca*, of Eastern Europe and Asia, and several others such as *Percarina* in Southern Russia and *Aspro* in the Rhone and Danube. *Cottus gobio*, the miller's thumb, and one or two other species of *Cottus*, and *Lota vulgaris*, the burbot, are also characteristic.

The fresh-water fish-fauna of a continent being determined partly by climate and partly by means of communication, it is not surprising to find that the fresh-water fishes of North America are more similar to those of the Euro-Asiatic region than to those of South America, the connection with the latter being geologically recent. The similarities are shown by the sturgeons, the salmonoids, the carps, the pikes and the perches, though among these there are of course minor differences. The European trout is absent, but there are numerous similar species west of the Mississippi, while to the east are species of *Salvelinus* or char. That the sturgeons and migratory salmonoids of the North Atlantic and North Pacific should ascend rivers of the east and west of North America as in Europe and Asia requires no explanation. These are not exclusively fluviatile fishes. Species of the carp family are as abundant in North America as in Europe, but the species and genera are mostly different; in the west *Leuciscus*, the commonest European genus, occurs, and also *Abramis*, the bream genus. The common pike occurs and another larger species as well as three smaller; there is also a species of *Umbra*. Perches are numerous but for the most part different from those of Europe, the common perch being represented by the yellow perch, *Perca flavescens*, while the other species are small and belong to genera unknown in Europe or Asia. On the other hand, there are important differences between the two regions. The Holostean Ganoids, three species of bony pike (*Lepidosteus*) and one of bow-fin (*Amia*), are peculiar to N. America. Of the carp family loaches are wanting and the

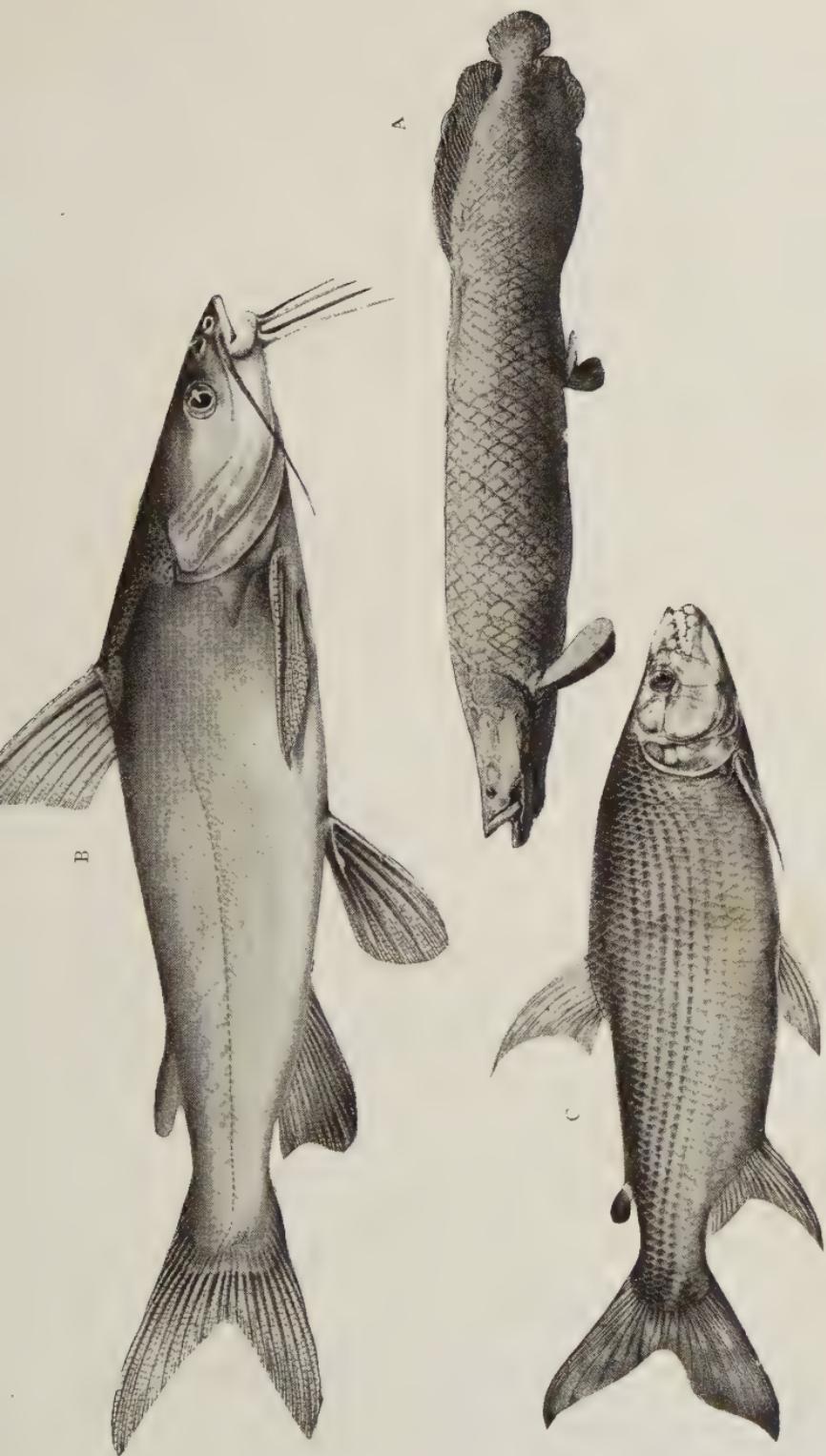
sub-family Catostomina are with one exception confined to this continent; Siluroids or cat-fishes are abundant, but it is a curious fact that they are confined to the regions east of the Rocky Mountains; they are known as channel-cats, *Ictalurus*, horned pout, *Amiurus*, and mad-toms which are quite small and belong to the genera *Noturus* and *Schibeodes*. These Siluroids were probably derived from South America. Cyprinodonts or toothed carps are abundant in the more southern parts, the range of this family having apparently extended from South America since the Isthmus of Panama connected the two continents; all the North American forms are carnivorous. There are numerous species, and many of them are abundant in individuals: the commonest genera are *Cyprinodon*, *Gambusia* and *Fundulus*, some species of the latter living on the sea-coast. The Amblyopsidæ, an offshoot from the Cyprinodonts including the blind cave-fish and its allies, are peculiar to North America. Of spiny-finned fishes (Acanthopterygii) the family Centrarchidæ or sun-fishes are peculiar to North America and are extremely abundant especially in the eastern rivers, the commonest genera are *Lepomis* and *Micropterus*, the latter known as the black bass; many of the species have a long backward development of the gill-cover, above the upper angle of the gill-aperture.

Of the tropical continents we may take South America first in order to contrast it with North America. Here there are no Ganoids, but there is one species of lung-fishes (Dipnoi), namely *Lepidosiren paradoxus*; true carps are entirely absent, and their place is taken by the Characinidæ, elsewhere found only in Africa; Siluroids or cat-fishes are also very abundant (Plate XXIII., B), several subfamilies being confined to this region as Callichthyinæ, Hypophthalminæ and Trichomycterinæ; the Loricariidæ, which are specialised Siluridæ, are also exclusively South American, and likewise the Aspredinidæ; the Gymnotidæ, containing the electric eel and its allies which are related to the Characinidæ, are found nowhere else. Among the soft-finned fishes (Malacopterygii) Osteoglossidæ are represented by *Osteoglossum* and *Arapaima*. (Plate XXIII., A.) South America is the head-quarters of the toothed carps (Cyprinodonts) of which the herbivorous genera *Poecilia*, *Mollenisia*, *Platypoecilus*, and *Girardinus* are found nowhere else. One species of Sym-

*branchus* occurs and the other two are Indian. Spiny-finned fishes (Acanthopterygii) are represented only by Cichlidæ the head-quarters of which are in Africa (15 of the genera with 140 species occur in South America, 30 genera in Africa), and by a few small species of the perch-like Nandidæ.

Africa in its fresh-water fishes has some features in common with South America and others in common with India, a fact which harmonises with its geographical position between those two regions. Characinidæ, as already mentioned, are abundant, the large and ferocious species of *Hydrocyon* or dogs of the water (Plate XXIII., C) corresponding to the fierce *Serrasalmo* of South America. *Citharinus*, the moon-fish of the Nile, on the other hand, is a harmless herbivorous fish which with allied species is confined to Africa. The whole of the family Mormyridæ is confined to Africa: it includes the eel-like *Gymnarchus* of the Nile, which reaches a length of six feet. Carps are abundant, many of the genera being the same as in India. Cat-fishes (Siluridæ) are also characteristic, some of the genera being also American, others also Indian; some genera are confined to Africa and among these is the electric cat-fish, *Malopterurus*. Africa possesses one lung-fish, *Protopterus*, closely similar to *Lepidosiren* of South America, while the only surviving fringe-finned ganoids (Polypteridæ) are found only in this continent. *Heterotis*, one of the Osteoglossids, is found only in Africa. A few species of toothed carps (Cyprinodonts) occur and extend into southern Europe, Spain, Italy and the Balkan peninsula. The most characteristic fresh-water fishes are the spiny-finned Cichlidæ which are especially well developed in Lake Tanganyika. *Lates* is a fresh-water species of the sea-perches (Serranidæ) occurring in Egypt. The Labyrinthici, distinguished by the labyrinthine organ above the gills, are common to Africa and Southern Asia. There are three species of serpent-head (*Ophiocephalus*), eleven of climbing perches (Anabantidæ), and one of the gourami family (Osphromenidæ).

The Indian region, including southern Asia as far as the island of Borneo, has no lung-fishes or Ganoids; it is the head-quarters of the carp family (Cyprinidae); cat-fishes (Siluridæ) are also very abundant with a large number of genera peculiar to this region. One genus of Cichlidæ occurs, namely, *Etroplus*. Labyrinthici are well represented; of Symbranchidæ *Amphip-*



A.—*ARAPAIMA GIGAS*  
B.—*GALEICHTHYS ASSIMILIS*, A CENTRAL AMERICAN SILUROID  
C.—*HYDROCYON GUATII*, AN AFRICAN CHARACINID



nous, the cuchia, is confined to India and Burma, and *Symbranchus* and *Monopterus* occur. *Lates* and some species of Nandidæ are the only other spiny-finned fishes (Acanthopterygians).

The Australian region, including Celebes and New Guinea, has the poorest fresh-water fish-fauna of all the regions of the world. It has one lung-fish, *Ceratodus*, of the carp-like fishes (Ostariophysi) only the cat-fishes (Siluridæ) are represented by a few species, the commonest being *Copidoglanis tandanus*. The Osteoglossidæ are represented by a genus peculiar to the region, namely, *Scleropages*, which extends to Borneo. There are two species of *Chilobranchus* belonging to the Symbranchidæ. The most abundant fresh-water fishes are so-called perches, members of the family Serranidæ, the most important of which is the Murray cod, *Oligorus macquariensis*, which attains to a weight of 50 lb., and the giant perch, *Lates calcarifer*, of Queensland is almost as large. In the south of Australia and in New Zealand occur members of two families of the pike Sub-Order (Haplomi) which are found only in the southern temperate zone; they are the Galaxiidæ and Haplochitonidæ. Eight species of *Galaxias* occur in New Zealand, one of them at least descending to the mouths of rivers, in order to spawn; the fry are known as whitebait. Several species are found in the south of Australia, several in Chili and Patagonia, and one at the Cape of Good Hope. Of the Haplochitonidæ, representing the trout of the northern hemisphere, one species of *Prototroctes* occurs in Queensland, one in South Australia, and a third in New Zealand. The only other native fish in the rivers of New Zealand are lampreys, eels, i.e., a species of *Anguilla*, and the New Zealand smelt *Retropinna* which ascends from the sea to spawn.

In the sea there are three regions differing greatly in their physical conditions and in their fish-fauna, that is to say the aggregate of species which inhabit them; these three regions are the littoral or coast region, the pelagic or surface of the ocean, and the abyssal. The three regions are not completely separated from each other as the fresh waters of South America are separated from those of Africa, but are continuous with each other, and the fauna of one is connected with that of the others by intermediate forms living in intermediate regions.

In the littoral regions there are various kinds of habitat to which different species are adapted ; there are fishes which live among the weeds which are attached to the rocks, such as the wrasses or Labridæ ; others which burrow in the sand like the sand-eels (Ammodytidæ) and weavers (Trachinidæ), or lie upon the bottom like the flat-fishes (Pleuronectidæ), the anglers (Lophiidæ), and the skates and rays (Batoidei) ; others which feed mostly on the bottom like the cod family (Gadidæ), others which live in shoals and feed in open water, either like the herrings (Clupeidæ) by the filtration method, or like the mackerel and the picked dog-fish (*Acanthias*), by preying on smaller fishes. These different habitats are not peculiar to any geographical region but occur in all parts of the world with similar fishes associated with them. Geographical restrictions of families or genera are determined for littoral fishes chiefly by temperature ; there is nothing to prevent the same species of littoral fish extending round all the coasts of the world, but in fact we find each zone of latitude characterised by its own fish-fauna. There are four great continental lines of coast running generally north and south, and along these there are four parallel series of littoral fishes ; in each of these, although species may be and usually are different, there is a general similarity between the fish population of different coasts in the same latitude. Thus we can distinguish Arctic fishes, those of the temperate zones, those of the tropical zone, and Antarctic fishes. There is even a certain degree of similarity between the fishes of the north temperate and south temperate zones, but less resemblance between the Arctic and the Antarctic. In the surface waters of the great oceans there is not so much difference between the temperature of different zones and no difference of habitat ; but even here there are differences of habits. Some pelagic fishes are large and powerful swimmers like the sharks and sword-fishes, others drift passively in the water like the sun-fishes, others even make their homes in the floating weeds like *Pterophryne* in the Sargasso. In the abysses the conditions of low temperature and great pressure are similar all over the world and sunlight is everywhere wanting ; but even here there are fishes which live on the bottom and others which swim actively in the water.

The most characteristic tropical fishes, especially in the

neighbourhood of coral reefs, are the Chætodontidæ and Pomacentridæ. Both of these families are perciform fishes of rather small size, short in proportion to their depth and in the case of the Chætodonts flattened from side to side ; they are extremely active and alert, and are remarkable for their vivid colours and conspicuous markings (see Frontispiece) ; bordered patches or ocelli and sharply defined bands of the strongest colours occur in the greatest variety in the different species, and the contrasts between these markings and the ground colour are often intense. In fact the riotous development of colour which is exhibited by tropical birds and butterflies is equalled if not surpassed by these fishes. In Chætodontidæ and several allied families the scales extend on to the surface of the dorsal and ventral fins, for which reason the group is often called Squamipinnes meaning scale-finned, and these fins are often prolonged backwards into tapering filaments. Species of *Chaetodon* occur in the West Indies and on other Atlantic coasts, and on the Pacific coast of Mexico, but they are most numerous in the East Indies. Some species of the family are excellent food-fishes, for example two species in the West Indies. The allied family Acanthuridæ is distinguished as the name implies by a knife-like movable spine on each side of the tail, from which they get the English name surgeon-fishes. *Teuthis* is a typical genus with species in the West Indies, on the west coast of Central America, and from India to Hawaii. In Scorpididæ the most remarkable fish is *Psettus sebae* which lives in the East Indies ; it is the deepest bodied of all fishes in proportion to its length, the vertical diameter at the broadest part being twice the length. A similar extension of the flat body in the vertical direction is characteristic of the species of *Platax*, known as the Sea-bats ; *Platax orbicularis* ranges from India to Japan ; this genus is included by some authorities in the Chætodontidæ.

Related to the Squamipinnes through the Acanthuridæ, from which they are derived by progressive modification, are the curious fishes of the Sub-Order Plectognathi, (*i.e.* with united jaw-bones), which are highly characteristic of tropical coasts. They are usually divided into three divisions : Sclerodermi (*i.e.* hard-skins) with a spinous dorsal fin, scales, and separate teeth ; Ostracionts, with no anterior dorsal, the scales replaced by bony

scutes united into an immovable carapace, and with slender teeth ; and lastly the Gymnodontes, in which the teeth are fused into a strong beak and the skin is either armed with spines or is naked. The Sclerodermi consist chiefly of the trigger-fishes and file-fishes which owe their names to the three dorsal spines of which the anterior when erected is fixed by the action of those behind it, and to the file-like character of the single spine in the second family. The trigger-fishes, *Balistes*, have strong teeth with which they break off corals and crush the shells of molluscs : the greater number of species occur in the East Indies extending to Japan and the Hawaiian Islands ; several species are common in the West Indies, others on the Pacific coast of Mexico, and one occurs in the Mediterranean. The tropical species are inedible, their flesh being poisonous. The File-fishes, *Monacanthus*, have a similar distribution but differ in habits, being herbivorous.

*Balistes* is known to devour numbers of pearl-oysters and in its turn is preyed upon by large rays ; recent investigations have shown that the pearl is deposited round the dead body of a parasite which is probably the larva of a tape-worm, and it has been suggested that the adult stages of this parasite live either in the *Balistes* or in the rays, or perhaps different stages in both. In consequence of the immovable carapace the movements of the trunk or coffer-fishes are very slow. Some of the species have the carapace developed into long horns projecting forwards above the eyes, and are hence known as cow-fishes. They are absent from the Pacific coast of America, common in the West Indies, extending across the Atlantic to the Gulf of Guinea, and common in the East Indies as far north as Japan. The Gymnodonts all have the curious habit of inflating the stomach with air and so distending the abdomen ; they are thus called globe-fishes or puffers ; when inflated they float at the surface belly upwards. In one family the beak is divided by a median suture above and below and they are therefore named Tetrodontidæ, the skin is either naked or spiny. In Diodontidæ the beak is undivided and these are all spiny ; the spiny forms are often called porcupine fishes. Some species of *Tetronodon* live in fresh water, occurring in the Nile and West African rivers ; many species are found on the east coast of America and the West Indies, others on the Pacific

coast of America, and others from Hawaii to India and in Japan. *Diodon hystrix* is found in tropical seas all round the world, other species are more limited in their range. The flesh of all the Gymnodonts is poisonous. The well-known Sun-fishes, although very different in shape, belong to the division Gymnodonts ; they are rather pelagic than littoral though often found near the coast ; they extend also into temperate regions, the common sun-fish (*Orthagoriscus mola*) being frequently taken off the British coasts. It is known to feed on larval fishes and is said to eat also jelly-fishes. Professor Grassi found larval eels in its stomach in the Straits of Messina, and believed these were swallowed at great depths, although it is usually seen swimming slowly at the surface. This species is cosmopolitan, while the short sun-fish, *Ranzania truncata*, is found in the Atlantic and Mediterranean and another species of the genus in the Pacific.

The Pomacentridæ are short stout-bodied fishes allied to the wrasses which are common on our own shores. (Frontispiece, A.) The wrasses or Labridæ themselves are likewise tropical and most of them brilliantly coloured, but they also extend into temperate regions ; they live in the neighbourhood of rocks and sea-weed. The Scaridæ, or parrot-wrasses, which are able, by means of their strong beak, to prey upon corals, are most abundant in the tropical Pacific, but there are nine species in the Atlantic, one of which is common in the Mediterranean.

Numerous other Acanthopterygians occur on tropical coasts, as the Serranidæ or sea-perches, Sciænidæ, Gerridæ and Pristipomatidæ, Mullidæ or red mullets and Callionymidæ or dragonets. Gadidæ are entirely absent, with the exception of a little pelagic form, *Bregmaceros*, which occurs in the Pacific but not in the Atlantic. Flat-fishes, on the other hand, are well represented, but by special genera, mostly belonging to the sub-families of sole-like or turbot-like forms. Of Malacoptyergii, Clupeidæ are abundant, the tarpons, *Elops*, *Megalops*, *Albula*, and numerous species of Murænidæ occur. The characteristic Elasmobranchs are Scyliiidæ only among the Selachii ; of the Batoidei, Pristidæ, saw-fishes, the Rhinobatidæ, Trygonidæ, sting-rays and Myliobatidæ eagle-rays.

In the Arctic regions the number of species is very small and forms a marked contrast with the large number in the

tropics. Of Acanthopterygians the chief families are Cottidæ, some of which reach a large size, Agonidæ, Cyclopteridæ or lump-suckers and sea-snails, and Blenniidæ. Characteristic genera are *Cottus* or the bull-heads, *Anarrhichas*, the cat-fish or wolf-fish, *Cyclopterus*, or lump-suckers, *Centronotus* or gunnels, and *Lycodes*. Gadidæ are also characteristic, especially species of *Gadus*, including the cod, *Brosnius*, the tusk, and *Molva*, the ling. The most northern of the Flat-fishes are *Hippoglossus*, the halibut, and species of *Pleuronectes* allied to plaice and dab. Physostomi are scarce, and represented only by the herring and a few other species of *Clupea* and by the salmonoid *Mallotus*, the capelin, which occurs in extraordinary numbers on the coasts of Greenland and Kamtchatka. Elasmobranchs are scarce, *Acanthias*, *Centrosyllium* and a species of skate being the only representatives; *Chimaera* also extends into Arctic regions.

The Antarctic fish-fauna shows a certain resemblance to the Arctic, some of the species being the same. Agonidæ and Scorpænidæ occur as in the Arctic, two of the genera, *Agonus* and *Sebastes*, being identical. Bull-heads (Cottidæ) are absent and in their place we find several genera of Nototheniidæ which, although in some species similar in appearance to the bull-heads of the north, are allied to the weevvers or Trachinidæ. *Lycodes* is found, but the lump-suckers and Arctic blennies are absent. One or two species of Gadidæ are found, namely *Lotella* and *Merluccius* or hake, but not the genus *Gadus*. Flat-fishes are scarce and belong to peculiar genera. Among the Elasmobranchs *Acanthias vulgaris* the common spiny dogfish is present and some species of skate (*Raia*) while *Chimaera* is represented by the southern form *Callorhynchus*. The re-appearance of certain Arctic species in the Antarctic region seems at first difficult to explain, but when we remember that temperature is the most important barrier to dispersal, and that there is a cold water connection between the waters of the two poles through the deeper parts of the oceans it seems quite possible that in the course of ages some specimens of an Arctic species might pass the tropical zone by travelling at a sufficient depth.

Having thus pointed out the most important special features of the extreme zones we shall not attempt to survey

the fishes of the temperate zones in general but shall merely try to convey an impression of the character of the fish-fauna of certain countries which are most likely to interest the British reader. In the first place we may compare the coast of Europe with the eastern coast of North America.

In comparing the Atlantic coasts of Europe and North America we have to consider not merely families and genera but species. The larger differences of families are few; for example, the marine Cyprinodonts such as *Fundulus* which occur on the American coast are wanting on the European side. The herring, cod, and haddock occur on both sides of the Atlantic in the north, and also the pollack, but the whiting is unknown on the American side, and the American hake is a different species of *Merluccius* from the European hake. Among the Pleuronectidæ or flat-fishes the species of the two sides are mostly different; the halibut occurs on both sides but the plaice is not found in American waters, it is replaced by a species called *Pleuronectes glacialis* or *glabra*. The valued sole and turbot are entirely wanting on the American coast, the brill is also wanting, but there is an allied species of small size and little value known as the window-pane from its thinness, technically named *Rhombus maculatus*; *Pseudopleuronectes americanus* is a species peculiar to America and allied to the plaice; the soles are represented only by small and useless species with rudimentary pectorals, the chief of which is the hog-choker (*Achirus lineatus*). Of other Clupeidæ besides the herring, American species are mostly different from the European: *Clupea brevoortia*, the menhaden, is a large fish and very abundant, it is valued for its oil, not as food; the American shad, *Clupea sapidissima*, is allied to but distinct from the European species, the pilchard is represented by distinct species and the sprat is absent. Among spiny-finned fishes (Acanthopterygians) the European families are represented, but usually by different genera or different species; the mackerel and the common horse-mackerel both occur; the John dory is entirely absent on the American coast, although an allied species occurs in Japan; the angler (*Lophius piscatorius*), on the other hand, is equally common on both coasts.

On the whole the fishes of the North Pacific are similar to those of the North Atlantic, and this is not surprising

when we consider that the two regions are at present in communication along the Arctic coasts and have been also connected in comparatively recent geological periods through the Isthmus of Panama, which is believed on geological evidence to have been depressed below the sea-level at the end of the Eocene period. The most remarkable peculiarity of the region is the presence of the family Embiotocidae or surf-perches, allied to the wrasses; all but two of the species occur on the Pacific coast of North America, the two exceptions being found on the coasts of Japan. No Embiotocidae are found in any other part of the world. True wrasses (Labridae) also occur both on the east and west coasts of this region as well as representatives of the parrot-wrasses (Scaridae). Another family peculiar to the region is that of the Hexagrammidæ allied to the Scorpænidæ, some of the genera being remarkable for the possession of several lateral lines, and all having only a single nostril on each side; they live on both sides of the region and are known in America as greenlings. Scorpænidæ themselves are abundant, especially species of the viviparous genera *Sebastodes* and *Sebastichthys*, viviparous reproduction being a characteristic feature of the Pacific coast. The European mackerel, *Scomber scombrus*, is absent, but the smaller and less valuable *S. colias* is abundant on the coasts both of California and Japan. The tunny is also fairly abundant. Carangidæ or horse-mackerels are represented by species of *Caranx*, *Trachurus*, and *Seriola* or yellow-tail. Most of the other families of Acanthopterygii are represented, though usually by species distinct from those of the Atlantic. Of the Gadidæ, which are less numerous than in the Atlantic, there is a cod, *Gadus macrocephalus*, only slightly different from the Atlantic species, two species resembling the pollack, and called *Theragra*, and a small form called tom-cod, *Microgadus*. The Pleuronectidæ are well represented, the halibut is abundant, and there are several other allied species referred to different genera; the flounder, plaice, dab, merry sole, and pole-dab are all replaced by representative species; soles are extremely scarce, only a few species allied to *Achirus* occurring in Japan. Of the Clupeidæ the principal are *Clupea pallasi*, as abundant as the herring in the Atlantic, and *Sardinella caerulea*, the Californian sardine. Salmon are more abundant in the North

Pacific than in the Atlantic, but they all belong to the genus *Oncorhynchus* of which there are six species, one of them confined to Japan. There are also two species of *Salmo* similar to the salmon-trout of Europe, one occurring in Kamtchatka, the other in Japan.

*South Africa.*—Of the Gadidæ the only European species which occurs in South African waters is the hake, *Merluccius vulgaris*, which is called the stockfish, and is one of the most abundant and commercially valuable fishes of the region. The name stockfish in Germany means dried cod, and was probably used because the hake was preserved in the same fashion by the early S. African colonists. The name kabeljaauw, which means cod in Dutch, and is applied in Holland to this fish in the fresh state, or as a species, in South Africa has been transferred to a fish of a very different species, not belonging to the Gadidæ at all, namely, the maigre, *Sciaena aquila*, which is also abundant and of great importance as a food-fish.

Only two other species of Gadidæ besides the hake occur in South African waters: one of these is *Motella capensis*, a kind of rockling of no great importance, and the other is called *Algoa viridis*. Another species, *Genypterus capensis*, which is sufficiently abundant and valuable to have a local name was formerly placed in the cod family; it is called the king klip-fish, and is now regarded as belonging to the Ophidiidæ, a family allied to the Blennies. There is a strong external resemblance in many points, especially in the tapering tail with confluent dorsal and ventral fins and absence of distinct tail-fin, between the extreme forms of the two groups represented by the Blenniidæ and Gadidæ respectively. The king klip-fish grows to a length of five feet, and its flesh is excellent for eating and well adapted for curing.

The maigre belongs to the spiny-finned fishes (Acanthopterygii), being the type of one of the numerous families of Perciformes. It has a very wide geographical range, being common in the Mediterranean and extending north to the coast of Sweden; it is occasionally taken on the south coast of England. Eastwards from the Cape it extends to the south coast of Australia, but is unknown on the eastern shores of the Pacific. Three other species which are plentiful in South

African waters and important as edible fishes are also perciform Acanthopterygians, namely, *Pagrus lanarius*, locally called the panga, *Dentex argyrozona*, the silverfish, and *Chrysophrys globiceps*, the white stumpnose. A considerable number of other perciform species are somewhat less abundant, but are valued as edible fish and have local names; of these the following are the most important: in the family Sciænidæ, besides *Sciæna aquila*, *Umbrina capensis*, the baardman and *Otolithus æquidens*, the geelbeck or Cape salmon; the former owes its name to the short barbel which it bears on the chin; *Dentex rupestris* bears the curious name of seventy-four, *Dentex filosus* is known as the sand-fish; in the family Sparidæ, *Cantharus blochii* is called the Hottentot, *Chrysophrys laticeps*, the red steenbras, *Chrysophrys gibbiceps*, the red stumpnose; *Pagellus mormyrus*, the zeverrim; *Pagellus affinis* the roi chorchor; in the Scorpænidæ *Sebastes maculatus* is called the sancord; of the gurnards or Triglidæ, *Trigla peronii*, the grey gurnard, and *Trigla capensis*, the red gurnard, are of some importance.

Of the Pleuronectidæ or flat-fishes the only group well represented is that of the soles. Neither our common sole nor any other species known to naturalists as British is found, but there is one species of sole in the strict sense, that is of the genus *Solea*. It is called *Solea bleekeri* and lives at moderate depths of about twenty fathoms. The genus *Synaptura* is distinguished from *Solea* by the fact that the marginal fins are confluent with the tail-fin instead of being distinct. Of this genus there are three South African species and one of them especially, *S. pectoralis*, was found in the trawling investigations instituted by the Government of Cape Colony to be very abundant on the Agulhas Bank at depths between thirty and forty fathoms. Almost equally plentiful was a species of *Cynoglossus* which differs from *Synaptura* in having the eyes on the left side instead of on the right, the fins being confluent as in *Synaptura*; the species is called *capensis*. A species of *Achirus* resembling the British solenette, and apparently of no more commercial value, occurs; it differs from *Solea* in having no pectoral fins. The British scald-fish is represented by a form which is only distinguished by minute specific characters: it has been named *Arnoglossus capensis*. The

genus *Pleuronectes*, including our valuable plaice, dab, flounder, lemon-sole, etc., is entirely absent, and the turbot and halibut groups are also unrepresented.

Grey mullets (Fam. Mugilidæ) are very numerous in South Africa both in species and in individuals. They are known for the most part in Dutch as harder, but *Mugil multilineatus* is called the springer, doubtless from its leaping habits. As in Europe, most of the species are estuarine, but many ascend into fresh water, and *Mugil constantiae* appears to be confined to fresh water.

The Trichiuridæ or hair-tails are represented, as in New Zealand, by *Thyrsites atun*, the snoek, and *Lepidopus caudatus*, called in Cape Dutch the kalk-visch; the former is large, abundant, and of great importance as a food-fish.

Of Carangidæ there are several species. One of the most abundant is *Caranx trachurus*, the horse-mackerel, which is common in British waters. Its local name is maasbanker. Although not marketable in England it is eaten at the Cape. *Seriola lalandii*, another species of the family known as the albacore or geelstaart (yellow-tail), is also caught for food in large numbers. *Tennodon saltator*, called the elft, is another species of this family which is common; it occurs on both sides of the Atlantic.

It has been stated that the European mackerel, *Scomber scombrus*, occurs at the Cape, but there is no satisfactory evidence of its presence to the south of the Equator. The closely-allied species, *Scomber colias*, which occurs on the coast of America and at St. Helena, differing from the English mackerel by the possession of an air-bladder, is very abundant. Species of *Cybium*, known in the United States as Spanish mackerel, are common, and several species of tunny or albacore occasionally approach the coast, namely *Thynnus pelamys*, the bonito, locally known as the katunker, *Thynnus alalonga*, the long-finned tunny, and *Pelamys sarda*, the pelamid.

The occurrence of *Coryphaena* (two species) is not surprising, as these fishes belong to the whole of the tropical and sub-tropical Atlantic.

A species of John dory, *Zeus capensis*, very similar to the European form is common.

*India*.—On the coasts of India the two chief species of

Clupeidæ are *Clupea palasah*, called the hilsa, which ascends all the large rivers in great abundance to spawn, and *C. neohowii*, the oil sardine, which does not enter rivers. Species of other genera of Clupeidæ are common: *Pellona*, *Opisthoterpus*, *Engraulis* or anchovy, and *Chatoessus*; the dorab, *Chirocentrus dorab*, is an allied species. *Elops* and *Megalops*, family Elopidae, or tarpons, also occur. Members of the eel families Anguillidæ and Murænidæ are numerous, but *Muraenesox*, which grows to ten feet in length, is the only one that is eaten. Gadidæ are absent, but Pleuronectidæ are numerous and valuable, especially *Pseudorhombus*, resembling the turbot, and *Cynoglossus* and *Sympnphura* which represent the Soles. One of the Scopelidæ, *Harpodon nehoreus*, is numerous on the Bombay coast and common in Bengal and Burma: it is dried and in that state known as Bombay duck. Of Acanthopterygii Day enumerates 616 species. The Indian mackerel, *Scomber kanaquita*, is abundant and *Thynnus pelamys*, the bonito, is common. Of Serranidæ or sea-perches the principal are *Serranus horridus* and *S. cooides*, the latter four to five feet long, and *Mesoprion*. Chætodontidæ are numerous, as in all tropical seas; the commonest are *Chaetodon*, *Chelmo*, *Ephippus*, noted for an enormous spherical bony mass on the back of the head, *Holacanthus*, *Heniochus* and *Drepane*; the last two are eaten; *Scatophagus* enters river mouths and, as its name (meaning dung-eater) implies, feeds on refuse. Mullidæ are numerous but are not prized like the red mullet of Europe; they are small species of the genera *Upeneus* and *Upeneoides*. Of Sparidæ or sea-breams there are numerous species of *Sargus*, *Lethrinus* and *Pimelepterus*, but the most plentiful and valuable is *Pagrus*. Species of the herbivorous *Teuthis* occur in vast numbers and are salted and dried. Maigres (Sciænidæ), hair-tails (Trichiuridæ) are used as food and also sword-fishes (Xiphiidæ). Of the Percesoces, *Sphyraena*, the barracudas, are large and numerous; Polynemidæ, remarkable for their long free pectoral rays, reach a very large size and are among the most valuable fishes in the market; *Poly-nema teru* is often seen in the Calcutta market six feet long, it is known as the mangoe fish and swarms into estuaries. Sand-smelts (Atherinidæ) and the grey mullets (Mugilidæ) are also abundant. Sharks and skates are captured for their fins which are exported to China, and for the oil from their livers. Electric

rays of the genera *Narcine* and *Astrape* swarm along the Meckram coast.

*New Zealand*.—The *Clupea sagax* of the South Pacific, which is abundant off the shores of New Zealand, is really a pilchard and does not exceed seven inches in length; by American ichthyologists it is placed with other pilchards or sardines in the genus *Sardinella*. An anchovy also occurs, not distinguishable from that of the European seas. *Gonorynchus greyi* is a soft-finned fish (Malacopterygian) almost confined to the southern hemisphere, it extends from the Cape to Japan; it is common in New Zealand, is from a foot to eighteen inches long and from the fact that it is found on sandy ground is known as the sand-eel. A species of the gar-fish family, *Hemirhamphus intermedius*, one of the half-beaks, is abundant. A species of grey mullet, *Mugil perusii*, is also common and valuable. The Gadidæ, or cod-like fishes are few and not very important; a species of hake (*Merluccius gayi*), the same which occurs on the coast of Chili, is not abundant, the red cod (*Physiculus bachus*) is common and valuable, and *Lotella callarias* almost equally so; these two genera are confined to New Zealand and Australia. Of Pleuronectidæ or flat-fishes, there are not many species, but those which do occur are fairly plentiful and valued as food; they are all distinct from the northern forms and one, *Peltorhamphus*, is peculiar to New Zealand. *Rhombosolea*, of which there are three species found also in Australia, represents the plaice and dab of our own seas. The remaining species are spiny-finned (Acanthopterygians); there is a species of mackerel, *Scomber australiensis*, which is probably identical with the widely distributed *Scomber colias*. As in South Africa the hair-tails (Trichiuridæ) *Thyrsites atun* and *Lepidopus caudatus* are valuable fishes in New Zealand; the former is called *barracouta* or *snoek*, it is caught with a piece of red wood with a nail driven through it and is largely exported in the dried state; its usual size is about three feet with a weight of 5 lbs. *Lepidopus caudatus* is known as the frost-fish because it is found cast up on the shore on exposed beaches after frosty nights; it is considered the most delicious fish in the country for eating and its price is as much as 2s. 6d. per lb.; it is usually about four feet long and 4 lbs. in weight. A large and characteristic species is the groper, also known by

the Maori name of hupuku ; it is called by Hutton and Hector *Oligorus gigas*, and stated to be closely allied to the Murray cod, *Oligorus macquariensis*, of Australia, but it is doubtful if it belongs to that genus ; its usual weight is about 45 lbs., but it may exceed 100 lbs. *Arripis solar*, called the native salmon, though having nothing to do with the Salmonidæ, belongs to the maigre family, Sciænidæ ; it visits the New Zealand coasts in summer and is 2 to 7 lbs. in weight. The southern family of Scorpидidæ is represented by the red snapper, *Scorpis hectori*. *Latris* is another genus occurring only in the southern hemisphere, being confined to New Zealand and Australia ; *Latris ciliaris*, called the moki, is abundant. *Chilodactylus macropterus*, the tarkihi, is common and is also a characteristic form of southern seas. Sparidæ or sea-breams are represented by *Pagrus unicolor* called the snapper, which is abundant. Of Carangidæ or horse-mackerels the cosmopolitan *Caranx tachurus* is as common as on the coast of England ; *C. georgianus*, the trevally, is more palatable for eating. *Seriola lalandii*, one of the yellow-tails known in New Zealand as haku or king-fish, is also well-flavoured. The red mullet family is represented by small and unimportant species of *Upeneoides* and *Upeneichthys*. One species of gurnard, *Trigla kumu*, is very abundant. True weevers are absent but represented by the Leptoscopidæ, one of which, known as rock-cod, *Percis colias*, is chiefly remarkable for its brilliant colours. Wrasses are represented by *Coridodax*, the kelp-fish or butter-fish, which like the gar-fish has bright green bones. Two species of the John dory family occur, *Zeus australis*, which scarcely differs from the European species, and *Cyttus australis*, which is of no value as food. *Genypterus blacoides*, belonging to the Ophidiidæ, is an eel-like fish with confluent vertical fins ; it reaches a length of five feet and a weight of 15 to 20 lbs. It is abundant on the more southern coasts of New Zealand and is caught in large numbers. It is known as ling and Cloudy Bay cod, and is used as food, but its flesh is not of the finest quality.

Space will not allow of a detailed enumeration of Australian fishes ; we can only point out that the coast of the island continent is of great extent, its northern half being within the tropics, while the southern reaches to the latitude of New Zealand. The fish-fauna therefore includes both tropical and temperate

forms ; the north coast belongs to the East Indian region and its fishes resemble those of India, while those of the south coast are similar to those of New Zealand. The east coast having the largest and the most advanced population, the fishes are naturally best known on this coast, in the middle part of which tropical and south temperate species mingle together. One of the most celebrated genera of Australian fishes from the biological point of view is *Phyllopteryx*, the species of which are sea-horses resembling the *Hippocampus* of Europe, but with many of the dermal bony plates produced into long processes which terminate in long irregular membranous appendages. These frond-like appendages have a close resemblance in the water to the fronds of the sea-weeds among which the fishes live ; all the pipe-fishes and sea-horses exhibit protective resemblance in colour and often in shape, but in none of them is the disguise so wonderfully developed as in *Phyllopteryx*.

*Pelagic Fishes.*—By this term is here meant those fishes which habitually live in mid-ocean near the surface ; there is no sharp separation between these and the littoral fishes, especially those of the latter which like the mackerel have pelagic habits, and true oceanic forms, either accidentally or habitually, may approach the coasts. The most characteristic forms are large sharks and spiny-finned fishes (Acanthopterygians) ; some Stomiatiidæ occur, including the Sternoptychidæ in this family ; among the Haplomi, Scopelidæ are numerous, and among the Percesoces, Scombresocidæ occur. *Hippocampus*, the Sea-horse, is one of the forms which drifts with floating weed and the Plectognathi are represented by the sun-fishes. The chief subdivision which can be made of oceanic habitats is between tropical and temperate, and as in other cases the number both of species and individuals is greater within the tropics. Of Elasmobranchs pelagic forms naturally belong to the Selachians or sharks, the Batoidei or rays being specially adapted to live on the bottom. The commonest oceanic sharks are species of *Carcharias*, thirty to forty in number, some of them twenty-five feet in length : these are tropical and sub-tropical and dangerous to man ; the blue shark, *C. glaucus*, is one of the commonest but not one of the largest, not exceeding fifteen feet in length ; smaller specimens are frequent on the south coast of England in summer.

*Galeocerdo* is another large genus of which one species, *G. arcticus*, is found only in Arctic seas. *Thalassorhinus* is another pelagic genus. *Sphyrna* or *Zygaena*, the hammer-headed sharks, are to a certain extent pelagic, but more frequently found living in deep water. Among the Lamnidæ *Charcharodon* is one of the largest and most dangerous of sharks, attaining a length of forty feet; it occurs in the tropics; *Lamna cornubica*, on the other hand, does not exceed ten feet and lives in the north temperate zone of the Atlantic and Pacific. The huge basking sharks, *Cetorhinus* or *Selache* in the Atlantic, and *Rhinodon* in the Pacific, are slow-swimming, harmless beasts, feeding by filtration by means of their gill-rakers; the latter is the largest shark known, reaching a length of fifty feet. *Laemargus borealis* is also a large shark, but does not seem to be dangerous; it lives in the Arctic Atlantic, occasionally wandering southwards. Of the Sub-Order Percesoces the Scombresocidæ contribute to the pelagic fauna the well-known flying fishes (*Exocoetus*), of which there are numerous species in the tropical Atlantic, Indian Ocean and Pacific, and some of the half-beaks allied to *Hemirhamphus* are found in mid-ocean. Many Stromateidæ of the same Sub-Order are pelagic, such as *Nomeus*, the Portuguese man-o'-war fish, so called from its association with the jelly-fish called Portuguese man-o'-war, *Seriolælla brama*, known as the warehou in New Zealand, common in the South Pacific, *Centrolophus*; the black fish, and *Lirus perciformis*, the rudder-fish, in the Atlantic which follow floating wreckage or driftwood and *Psenes*, of which there are several species found in tropical ocean currents, allied to *Nomeus*. The Sternoptychidæ, *Sternoptyx*, *Argyropelecus*, and *Polyipnus*, provided with numerous luminous organs, are most probably pelagic fishes living at some depth in the daytime and coming to the surface at night. Many Scopelidæ, such as the species of *Scopelus* or *Myctophum* itself, have similar habits and also possess luminous organs. Of the spiny-finned fishes (Acanthopterygians) the most characteristic are the dolphin-fishes *Coryphaena*, and the sword-fishes, Xiphidæ and Histiophoridæ; these are active and powerful swimmers which prey upon other fishes, the dolphins being the natural enemies of the flying-fishes. Many species of the Scombridæ or mackerels are pelagic, and in fact it may be

said that the majority of the division Scombriformes have pelagic habits, all the spiny-finned fishes hitherto mentioned belonging to this division. The chief Atlantic tunnies are *Thynnus thynnus*, the common tunny, *Thynnus alalonga*, the albacore or germon, *Thynnus pelamys*, the bonito, *Pelamys sarda*, the short-finned tunny, and *Auxis rochei*, a smaller fish, the plain bonito. Many Carangidae or horse mackerels are oceanic, for example *Naucrates ductor*, the pilot fish, species of *Caranx*, *Trachynotus* and *Seriola*, and *Lichia glauca*, which has been taken on the English coast. The Trichiuridae or hair-tails seem to show a transition from active pelagic to sluggish abyssal habits; some like *Thyrsites* are found at the surface and have well-developed tails, while others like *Gempylus* and *Trichiurus* have a narrow slender body and tapering degenerate tail; active pelagic fishes always have a deeply forked caudal fin like the tunnies and the sword-fishes. *Luvarus imperialis* and the various species of Bramidae are short-bodied Scombrids which seem to have a great range in depth; as they are rare fishes their habits are little known. The same may be said of the opah, *Lampris luna*, which is oceanic and widely distributed. The flying gurnards *Dactylopterus*, are Acanthopterygians, which are adapted for short flights in the same way as the true flying-fish *Exocoetus*; they are chiefly found in the tropical Atlantic and Indian Oceans, one species being fairly common in the Mediterranean. The sargasso-fish, *Pterophryne*, has its home in floating weed such as the sargasso of the Gulf stream and the weeds of the Japanese Kuro Siwo or Black Current, and in the same conditions are found species of *Hippocampus* or sea-horse. Finally may be mentioned the sun-fishes, the pelagic, extremely modified form of the Plectognathi; they are passive fishes which drift with the currents and seem to descend to great depths or to rise to the surface at will.

*Abyssal Fishes.*—The deep sea is often taken to commence at a depth of 200 fathoms, as that is about the limit to which the light of the sun penetrates; it is certain that fishes which live habitually beyond this depth usually show some structural differences, such as the enlargement of the dermal sensory tubes, from those which live in shallower water. Almost every littoral species which lives on or near the bottom has a restricted range of depth: we do not find the same species usually at a depth

of 20 fathoms and at a depth of 200 or more, but some species are known to have a very wide range of depth, which may be horizontal in bottom fishes or vertical in free-swimming forms. The greater part of the great oceans, the Atlantic, Pacific, and Indian, is over 2000 fathoms in depth, and a somewhat smaller portion, especially in the Atlantic, is from 1000 to 2000 fathoms; the parts over 3000 fathoms are of small extent, and there are only three deep holes off Japan, New Zealand and the West Indies where the depth of 4000 fathoms is exceeded. The greatest depth at which fish have been taken is nearly 3000 fathoms, to be precise 2949 fathoms, in the western part of the North Atlantic by the American investigation vessel *Albatross*, and the fish in question was *Melamphaes beanii*, a species of the family Berycidæ, the most primitive of the spiny-finned fishes (Acanthopterygians); at the same haul was taken *Stephanoberyx gillii*, a type of a family placed by Boulenger in the Sub-Order Haplomi on account of its abdominal pelvic fins, but resembling the Berycidæ in many respects. It would be well to confine the term abyssal to fishes taken at depths of more than 1000 fathoms, and to form a separate group for those found between 200 and 1000 fathoms. While many families include abyssal members there are some families which are found only in the great depths, and although we have maintained that the most primitive forms are usually inhabitants of fresh water, some of these exclusively deep-sea fishes belong to the primitive soft-finned Sub-Order Malacopterygii, or at any rate show primitive characters, a fact which in the present state of knowledge we do not attempt to explain.

The Alepocephalidæ or Fox-heads belonging to the Malacopterygii are all abyssal; there are about thirty-five species distributed in the Atlantic, Pacific, and Indian oceans mostly between 1000 and 2000 fathoms, though they have been taken frequently at less depths and occasionally at greater. They resemble in structure the Clupeidæ and Salmonidæ. The families Halosauridæ and Notacanthidæ, placed by Boulenger in the Sub-Order Heteromi, are also exclusively found in deep water, but many of the species occur at depths somewhat less than 1000 fathoms; *Halosauropsis rostratus*, however, was obtained by the *Challenger* in the Atlantic at 2750 fathoms. *Lipogenys*, also from the Atlantic, is closely allied to the

Notacanthidæ. Several families of the soft-finned fishes (Malacoptyergii) contribute more or less largely to the abyssal fauna. In the Stomiatiidæ, considered as distinct from the Sternoptychidae, many of the species are certainly inhabitants of deep water but with regard to others, as to many other species in other families, the records of the depths at which they have been obtained are open to serious doubt. The dredge or trawl was open during its ascent to the surface, and therefore a fish taken in it might have been captured at any depth between the bottom and the surface in the course of the ascent. When a fish like *Astronesthes niger* is frequently taken at the surface and also is found in a dredge which has been on the bottom at a depth of 2500 fathoms it is difficult to believe that it can actually live under such different extremes of temperature and pressure, and such species must for the present be considered to be pelagic, though ranging perhaps to some hundreds of fathoms from the surface. The other species of the Stomiatiidæ seem to be truly abyssal, some of them, such as *Malacosteus indicus*, being among the most extraordinary deep-sea fishes known. The genera are numerous, *Stomias*, *Macrostomias*, *Echiostoma*, *Opostomias*, etc.; they have elongated bodies with small tail-fins, large mouths and formidable dentition, with a long barbel under the chin. The Sternoptychidae having a compressed body and silvery colour have more the appearance of pelagic than of deep-sea fishes, but some of them range, according to the records, from 100 or 200 fathoms to depths between 1000 and 2000 fathoms; it is doubtful if any of them descend to more than a few hundred fathoms from the surface. Belonging to the family Salmonidæ are four genera which live in deep water; of these *Argentina* occurs in moderate depths down to 200 fathoms in the Atlantic while the numerous species of *Bathylagus* are true abyssal forms, most of them having been taken only at depths between 1000 and 2000 fathoms. Of the eels or Apodes three families are inhabitants of the greatest depths, and it can scarcely be doubted that they live actually at the bottom, though here again we have the difficulty of the enormous range of depth of the same species. These families are the Nemichthydæ, Synaphobranchidæ, and Saccopharyngidæ. *Nemichthys* has been taken in the Atlantic at depths from 216 to 2369 fathoms but most frequently at the more moderate depths.

*Saccopharynx* has only been once taken at the bottom from a depth of 898 fathoms; other specimens have been taken at the surface but floating in a helpless condition in consequence of swallowing a fish too large for them. Many genera of the Anguillidæ are also abyssal, extending down to 2500 fathoms; *Simenchlys parasiticus* occurs in the Atlantic from 200 fathoms to 1093 fathoms; it has a suctorial mouth and burrows into the flesh of living halibut and other fishes. When we consider the range in depth of some of these forms we must remember that the common eel migrates from rivers and ponds to a depth of over 500 fathoms in the sea, although this does not dispose of the question whether the same species can live indifferently at the surface and at depths of more than a thousand fathoms; the common eel does not return from its migration. Several less modified species of Anguillidæ are taken at moderate depths, *Myrus pachyrhynchus* for instance between 500 and 800 fathoms off Morocco. Among the Haplomi the family Scopelidæ includes both common pelagic forms and abyssal; some species of *Scopelus* (*Myctophum*) and of *Chlorophthalmus* have been taken only within a hundred fathoms from the surface, and at night are frequently taken at the actual surface; other species have been taken only at great depths. *Synodus*, a little fish resembling *Scopelus* but without luminous organs, has been taken only near the surface and down to 150 fathoms. Other genera, e.g. *Bathypterois*, *Bathysaurus*, *Scopelengys* and *Ipnops* are entirely abyssal. *Bathypterois* has the upper rays of the pectorals and the first ray of the pelvic fins much elongated; different species have been taken in all the great oceans at depths from 500 to 2500 fathoms. *Bathysaurus* has ordinary fins, and a large mouth with sharp teeth; it has been taken at depths down to 2385 fathoms in the Atlantic and Pacific. *Ipnops* has been taken only at very great depths, from 1300 to 2150 fathoms, and is one of the most extraordinary deep-sea fishes in the absence of eyes and the presence in their place of organs supposed to be luminous. *Rondeletia* and *Cetomimus*, taken at depths between 1000 and 1600 fathoms in the North Atlantic, are considered by Boulenger to be allied to the Scopelidæ. *Cetomimus* owes its name to its absurd resemblance in shape of body, small eyes, and large curved mouth, to the Greenland whale, although it is only five inches long, *Rondeletia* having

large eyes and a blunt snout is more normal. Of the Anacanthini the Macruridæ are all inhabitants of deep water and some of them exclusively abyssal; *Macrurus* itself, characterised by its long tapering tail, large eyes, and projecting pointed snout, is represented by numerous species ranging from about a hundred to nearly 2000 fathoms. The other genera are not very different in structure; the species found at the greatest depths is *Lionurus filicauda*, taken by the *Challenger* at 1375 and 2650 fathoms off the east and west coasts of the southern extremity of S. America. Some species of the cod family (Gadidæ) also are abyssal, *Melanonus gracilis*, for instance, was taken by the *Challenger* at 1957 fathoms in the Antarctic.

Among the spiny-finned fishes (Acanthopterygii) the most characteristic of the abyssal families are the Ceratiidæ and Malthidæ belonging to the Sub-Order Pediculati and allied to the anglers or Lophiidæ, and the Zoarcidæ, which are sometimes divided into several families, the abyssal forms being called Brotulidæ.

The abyssal sea-devils, as the Ceratiidæ were called by Günther, differ usually from *Lophius*, the common angler, in being compressed from side to side instead of being flattened, but they possess the characteristic dorsal tentacles, one or more, representing rays of the first dorsal fin, and the anterior tentacle often terminates in a luminous organ which probably acts as a lure to other abyssal fishes. One of the most modified forms is *Dolopichthys*, a small fish only two to three inches long, in which the fins are rudimentary and the tentacle is long and jointed with a luminous organ at its end; it was discovered at 770 fathoms off the Pacific coast of Central America. The greatest depth at which fishes of this family were obtained was 2450 fathoms, at which a specimen of *Melanocetus murrayi* was captured; in this fish, also a few inches long, there is only one tentacle above the mouth and it shows no luminous organ. *Mancalias uranoscopus*, a species with large luminous organ was taken by the *Challenger* at 2400 fathoms. Malthidæ, in which the body is depressed and the tentacle reduced to a papilla, have been taken down to 1270 fathoms. *Chaunax* is placed among the Antennariidæ; it has a beautiful red colour and is found at moderate depths.

Among the Brotuloids are two genera which are almost the

only abyssal fishes which are totally blind, the eyes in these being absent. It is probable that they live buried in the mud. One of these, *Typhlonus nasus*, was taken at 2150 to 2440 fathoms, the other *Aphyonus* at 955 to 1400 fathoms. The species of abyssal Brotuloids are numerous, and many of them come from the greatest depths; they usually have the sense-tubes, especially on the head, greatly enlarged and transparent, the sense organs within being large and conspicuous. A few other spiny-finned families have members at moderate depths less than 1000 fathoms, such as Scorpænidæ, and Cyclopteridæ, or lump-suckers; in fact species of *Paraliparis* of the latter family range to 1800 fathoms, but the most peculiar and characteristic forms are those mentioned.

Chimæroids live for the most part in deep water, *Harriotta* having been taken only at depths between 707 and 1080 fathoms. Of Elasmobranchs few are really abyssal, only two or three species of *Raia* having been taken at depths over 1000 fathoms. *Centrophorus* is the bathybial genus of the sharks or Selachians, two of its species passing beyond the 1000 fathom line. Several members of the order, however, extend beyond 200 fathoms.

## CHAPTER IV

### CONDITIONS OF LIFE AND PHENOMENA OF SEX

Food and feeding. Relations to temperature, light and salinity. Influences of seasons; migrations, hibernation and aestivation. Association and commensalism, parasitism. Relations of sexes, sexual dimorphism.

AS so many fishes feed on fishes it seems at first difficult to understand how their vast hosts are maintained and why they have not long ago become extinct in consequence of mutual slaughter. Ultimately all animal life depends on the material and energy supplied by plants, which alone are able by the aid of the rays of the sun to produce organic substances from inorganic materials. Few fishes are however directly herbivorous; the Australian lung-fish *Ceratodus* devours water-weeds, and it is usually stated that it does this for the sake of the minute animals living among them, but no reason is given for the conclusion that it does not digest the weeds themselves; in the Zoological Gardens of London, *Ceratodus* eats lettuce as a regular part of its diet. Grey mullets certainly feed partly on the small green algae which coat the surfaces of stones and wooden piles in harbours and estuaries and also on mud, which they swallow for the organic matter, largely consisting of diatoms, which it contains; these fishes have feeble teeth or none, and the stomach forms a strong gizzard like that of a bird. The Cyprinidæ or carps have no teeth in the jaws at all, and the teeth in the pharynx vary with the nature of the food; many of them feed on mud and vegetable substances; in these the pharyngeal teeth are adapted for mastication and the intestines are long and convoluted. *Dorosoma cepedianum*, belonging to the Clupeidæ and living in the Mississippi, is commonly called the hickory-shad because the stomach forms a gizzard of the size and shape of a hickory nut; it and its allies feed on mud, they have a small contracted toothless mouth, and their nourishment must depend largely on

diatoms and other vegetable substances in the mud. The Cyprinodonts are divided into two groups, carnivorous forms in which the intestine is short, and those which feed on vegetable substances and mud and have long convoluted intestines. The latter form the sub-family Poeciliinæ including *Poecilia*, *Mollisnia*, and two other genera. Some of the Labridæ and their allies the fresh-water Cichlidæ are herbivorous, and also some of the Sparidæ or sea-breams.

With the comparatively few exceptions mentioned above the fishes feed on other animals ; the larger and more voracious forms capture and devour smaller and weaker fishes, these weaker or more peaceful forms feed on invertebrates of various kinds, molluscs, crustaceans, and annelids chiefly. The majority of fishes therefore depend on the vegetable kingdom only indirectly, the invertebrates feeding on plants. In the sea, with the exception of the sea-grass, *Zostera*, the only conspicuous plants are the algæ or sea-weeds which are attached to the rocks round the shores. As no light penetrates beyond two hundred fathoms there are no plants living beyond that depth. The number of invertebrates which feed on the larger sea-weeds is small, the principal being the herbivorous gastropods such as the periwinkle. The great class of Lamellibranchia or bivalve molluscs such as the oyster and mussel are nourished by microscopic particles which they filter from the current of water which is continually passing through the branchial cavity; these particles are chiefly the microscopic unicellular plants called diatoms. Diatoms are abundant everywhere around the coasts and form a sediment on the surface of mud deposits, so that they contribute largely to the nourishment of mud-eating invertebrates such as annelids and Holothurians or sea-cucumbers. In the vast extent of open ocean beyond the 200 fathoms line the rôle played by diatoms is still more important. In the upper stratum of the ocean from the surface to 200 fathoms there is a teeming life of animals and plants ; the latter are all microscopic and consist chiefly of diatoms, the animals are of various sizes and various invertebrate classes, but the most abundant are small crustaceans of the kind called Copepoda. This world of floating life is called the plankton, and is the basis of oceanic fish-life. The Copepods and other animals are all dependent directly or indirectly on the diatoms,

and the diatoms owe their life, like other plants, to the sunlight. These microscopic plant-cells supply the place in the surface waters of the ocean of the grass and other vegetation on the land-surface, and it has been truly said that as all flesh is grass so all fish is diatom; for the smaller gregarious fishes such as the Clupeidæ feed chiefly on the small Copepods, and the Copepods feed on diatoms, while the gregarious fishes are preyed on by the larger predatory forms. The fishes which feed on plankton have an efficient filtering mechanism formed by the gill-rakers, a double series of cartilaginous or bony rods which project forwards from each branchial arch; these rods form a sieve completely covering each of the gill-clefts, for they extend across the interval between each gill-bar and the next. The water therefore which enters the mouth is strained as it passes out between the gill-rakers, and any solid particles it may contain are left in the pharynx. The sufficiency of the plankton as a supply of nutriment is shown by the fact that the largest sharks, *Selache*, the basking shark, and *Rhinodon*, feed entirely by the method of filtration through the gill-rakers. There are, however, some tracts of the ocean which have a floating vegetation of large algæ, as mentioned above, namely the region of the sargasso in the Atlantic and a similar region in the Kara Shiwo or Black Current in the Pacific. The sargasso has a fauna of its own, but how far the weed supplies food as well as shelter or concealment is a matter which has not been minutely investigated. Abyssal fishes, since plant life is entirely absent in the great depths, are ultimately dependent for nutrition on the organisms which fall within their reach from the surface waters; many of them, as mentioned in the general description of them already given, are predatory, and live upon other fishes of the same habitat, but the latter must feed on invertebrates such as Crustacea and these again upon the organic matter derived from surface life.

The range of temperature under which different fishes live is very great. In fresh waters fishes extend northwards until they are stopped by the freezing of the water, and even exist in waters which are only liquid for a few months of the year; *Dallia pectoralis*, a species allied to the pike, lives in the north of Alaska and seems to be accustomed to be frozen in the ice for considerable periods in winter; one which was swallowed in the

frozen condition by a dog was thawed by the heat of the stomach and vomited alive. In the sea in Arctic regions many fishes live at or near the freezing-point and from this lower limit fishes are found at all temperatures up to the greatest heat of tropical swamps where *Protopterus* and *Lepidosiren* occur. In the ocean abysses the temperature is not far from freezing-point, varying from  $28^{\circ}$  in the Atlantic to  $35^{\circ}$  in the Pacific. Fishes have also accommodated themselves to all intensities of light, from that of the surface of the sea in the tropics to the absolute darkness of the Kentucky caves. The ocean abysses of the sea are evidently not dark, although the sunlight never penetrates to them, for most of the bathybial fishes have large eyes and pigmented skins; only a few species are blind, these being probably burrowing forms. The light in these depths is derived from the luminous organs of the fishes themselves and other animals, and it may be limited to the immediate neighbourhood of the animals which produce it, but in any case it is enough to enable the eyes to perform their function, while *Amblyopsis* in the caves of Kentucky, and the Cuban cave-fishes *Stygicola* and *Lucifuga*, have lost their eyes altogether, and also the pigment of the skin.

In the fresh waters the quantity of soluble salts is at a minimum, and the density is not appreciably different from that of pure water; fresh-water fishes, therefore, live in a medium less dense than their own blood. In the sea the density of the open ocean at the surface is 1.027, at the bottom, 1.029; this is exceeded in the Red Sea, where the density is 1.030. Between these extremes all intermediate densities occur and in all of them fishes live; in the Black Sea, for example, in consequence of the large rivers which flow into it, the density is only 1.025 and in the Baltic it is less, while in every estuary there is a gradual transition from the salt water of the sea to the fresh water of the river. The density of 1.027 in Atlantic water corresponds to the presence of 3.5 parts of dry salts per cent in solution, and this is far above the proportion present in the blood or flesh of the fish; it is an obvious fact that the flesh of marine fish is not so salt as the water in which they live, and therefore the living cells of the skin have the power of preventing the passage of the salt from the sea-water into the body of the fish. This power is due to an ad-

justment of the action of the living tissues to the salinity of the medium, and therefore fresh-water fishes, such as the carp or perch, are killed when placed in sea-water, and conversely sea-fishes such as the haddock or mackerel are killed by fresh water. Many fishes, however, like the salmon and eel, are able to pass from the sea into fresh water and vice versa in their regular migrations, and many littoral fishes such as the sticklebacks and grey mullets can live either in fresh or salt water; in these cases, however, the change must usually be made gradually. There are some lakes in which there is such a large quantity of saline and alkaline matter in solution that no fishes can live in them, for example, the Dead Sea in Syria, and some of the lakes in Utah, North America.

The annual changes of physical conditions with the seasons have their effects on fishes as on other animals, the resulting migrations or changes of habit varying with the species and with the habitat. Pelagic fishes within the tropics and bathybial fishes are little affected or not at all, while littoral and fresh-water species often exhibit remarkable annual cycles in their habits.

The ultimate cause of migrations is the seasonal change of temperature, but the immediate cause may be reproduction or food. Definite migrations are exhibited along the coasts chiefly by gregarious fishes, for example, the herring. The greatest change of temperature occurs in the shallow waters near the land, and on the coast of Europe we observe in summer a movement of fish from the sea towards the coast and from the south to the north. Mackerel are unable to bear cold water; on our coasts they are found at the entrance of the English Channel even in winter but in summer as the shore waters become warmer, they approach nearer land and travel up the Channel to the North Sea. They spawn a few miles from the coast in May and June and then travel, in search of the young of other fishes on which they feed, into bays and estuaries, so that in August and September they are caught with the seine drawn on to the beach. From November to May there are no mackerel in the North Sea. The anchovy is another good example of temperature migration; it annually passes up the English Channel to reach the Zuyder Zee and the estuary of the Schelde, where it spawns in summer, and

departs again to the south in winter, these shallow waters of the coast of Holland being warmer in summer than the Channel. The pilchard approaches the coast of Cornwall, which is the northern limit of its range, in summer and autumn from July to Christmas, and retires to the south in the colder months ; its object is food not reproduction, for it is known to spawn from twenty to fifty miles from the land and those which are caught near the coast have the reproductive organs undeveloped. A curious fact about the pilchard is that the young fish which are caught on the coasts of France, Spain, and Portugal, and preserved as sardines, are not usually found in large numbers on the Cornish coast, only the adults travelling so far north. These are examples of southern species which shed pelagic eggs and have no special spawning places, but in their search for food follow the summer to the northward ; similarly northern species extend their range more to the southward in winter. In the case of the herring, which is a northern species, the chief migration is for the purpose of spawning and the movements cannot be directly correlated with temperature ; the spawn of herrings is adhesive and demersal, and is deposited on stony banks at moderate depths near the coast. Any given ground is visited annually, but the season for each ground is different, and there is scarcely any month in the year in which spawning is not taking place off some part of the British coasts. A broad division can be made between herrings which spawn in winter nearer to shore and those which spawn in summer in deeper water. Thus off the east coast of Scotland the spawning season which marks the end of the summer fishing season is the month of August, the warmest part of the year, while on the north coast of Cornwall spawning takes place in the coldest month, namely January. The winter herring at various stages of growth enter estuaries in large numbers, for example the Forth, the Thames and the Tamar. The movements of herring between the spawning seasons are not very completely known but there is good reason to believe that they do not go very far from the coast, and it is probable that they congregate in shoals at the spawning season more than at other times.

The most definite and extraordinary migrations are those undertaken by marine species which ascend rivers to deposit their spawn or those fresh-water forms which descend to the

sea for the same purpose. The former are called anadromous and the latter katadromous. The most important anadromous fishes are species of *Salmo* in the North Atlantic and *Oncorhynchus* in the North Pacific. The salmon, *Salmo salar*, may enter rivers at almost any time in the summer but there is usually a more definite migration in autumn, and the fish travel up stream to the highest parts of the rivers, jumping through rapids and falls which are not too high, till they reach the gravelly beds in which they make their redds, that is to say in which the female scoops out furrows for the reception of the eggs and heaps gravel over them. The fish take little or no food during this migration and the males fight fiercely together; their condition therefore deteriorates greatly and when the spawning is over they are exhausted and emaciated, with discoloured and usually abraded skins. In this condition many die of exhaustion or fall victims to disease, in which they are attacked by the salmon fungus, *Saprolegnia ferax*. A certain proportion, however, return to the sea, recover their health and vigour and spawn repeatedly. The following account is given of the king salmon or quinnat of the Pacific coast of North America by American ichthyologists: This great fish, *Oncorhynchus yschawitscha*, spawns in November at the age of four years and the average weight of 22 lbs. In the Columbia river it begins running with the freshets in March and April; it spends the whole summer without feeding in the ascent of the river. By autumn the fish have reached the mountain streams of Idaho, greatly changed in appearance, discoloured, worn, and distorted. The males are hump-backed, with sunken scales and greatly enlarged, hooked, bent, or twisted jaws, and enlarged dog-like teeth. On reaching the spawning grounds, which may be 1000 miles from the sea in the Columbia, over 2000 in the Yukon, the female deposits her eggs in the gravel of some shallow brook; the male covers them and scrapes the gravel over them. Then both male and female drift, tail foremost, helplessly down the stream; none, so far as certainly known, ever survive the reproductive act. The same habits occur in five other species of *Oncorhynchus* in the North Pacific, but in these the fish do not start so early nor run so far. The size and weight of the quinnat ascending rivers varies enormously, some of the males being only eight inches long, but the smallest

females being eighteen inches ; the largest reach 40 to 60 lbs. in weight and specimens of 80 or even 200 lbs. have been recorded. It is not known that all these fish are of the same age, some may become mature when only a year old, others at two years or several years, but there is no evidence that any survive after spawning. In the case of *Salmo salar* in the Atlantic, the young, called parr, remain in the rivers for the first year and then in the following spring, or after two or three years, they become smolts and descend to the sea. It was formerly believed that the smolts returned to spawn in the autumn of the year in which they descended, but it has recently been shown that they remain more than a year in the sea.

The migration of the eel, that is to say, of the European *Anguilla vulgaris* and of other species of *Anguilla* in other parts of the world, resembles that of *Oncorhynchus*, except that it is in the opposite direction, but a description of it is given in a special section devoted to the life-history of the eel. The majority of the sturgeons, that is, species of *Acipenser*, are anadromous, the common sturgeon spawning in European rivers about July, but in North America in the Delaware in May. Among the Clupeids or herring family there are several anadromous species, such as those commonly called shads, *Clupea alosa* and *C. finta* in Europe, and *C. sapidissima* in North America. The Galaxiidæ are mostly confined to fresh water in the southern hemisphere, but *G. attenuatus* in New Zealand descends to the sea to spawn. Whether the katadromous or descending habit is due to a fresh-water species acquiring the habit of spawning in the sea, or a marine species ascending rivers in search of food, must be decided by the affinities of the species in each case ; the flounder is evidently an example of the latter case, it ascends estuaries to brackish, or even fresh water, but always descends to the sea to spawn.

Many fresh-water fishes become more or less torpid in the winter in northern and perhaps in southern latitudes. They do not fall into a completely unconscious condition like reptiles and some mammals, but cease to feed and hide in sheltered places ; this is the case with many of the carp family (Cyprinidæ) ; the common eel remains buried in the mud or in holes. Marine fishes are not known to hibernate as a rule, they usually retire to deeper water where the reduction of temperature is not very

great, as for example in the case of the sole. There is evidence, however, that young plaice remain buried in the sand in the shallow water in winter. On the shallow grounds off the Dutch and German coasts of the North Sea small plaice are taken in enormous numbers in spring and summer, but are not to be caught with the trawl in January, February and March, and it was observed in the aquarium at Cleethorpes in Lincolnshire that such small plaice never showed themselves in the cold weather, but emerged from the sand and were eager for food the first warm day in spring. Æstivation or the assumption of a torpid condition in the dry season is not uncommon among the fresh-water species of the tropics. The lung-fishes (Dipnoi) *Protopterus* in Africa and *Lepidosiren* in South America, living in swamps which dry up in the rainless part of the year, burrow into the mud and remain torpid during the dry season, while *Ceratodus*, inhabiting the deep water-holes of the rivers of Queensland which seldom or never dry up completely, does not æstivate in this manner. *Protopterus* coils itself up at the bottom of its burrow and becomes surrounded by a layer of slime secreted by the skin; the slime hardens and forms a closed capsule perforated only by a hole opposite the fish's mouth for the entrance of air to the lungs. Specimens of this fish have been frequently imported into England, encased in their cocoons of dried mud and slime. On arrival the mass of mud has been softened with warm water, and the liberated fish has revived and lived in an aquarium for months or years. *Lepidosiren* makes a similar burrow but the mouth of it is closed by a lump of clay perforated by several holes. It is interesting that those fishes of the Order Teleostei which æstivate in a somewhat similar way have also organs for breathing air, and these must have been evolved in response to similar needs in similar modes of life; but in these the organs are not lungs or air-bladder but are accessory organs connected with the gill-chamber. The Ophiocephalidae or serpent-heads are abundant in India and Ceylon, and also in China and tropical Africa; when the water of the pond or "tank" in which they are living dries up they simply bury themselves in the mud and remain there till the drought is passed. The climbing perches (Anabantidae) and gouramis (Osphromenidae) survive in the mud of dried up ponds in the same manner. Among the cat-fishes

(Siluridæ) of Africa and India, *Clarias*, *Heterobranchus*, and *Saccobranchus* have accessory respiratory organs, and *Clarias* at least is known in West Africa to spend the dry season in burrows, although it does not appear to be torpid all the time, but crawls about at night in search of food. Among the eel-like Symbranchii, *Symbranchus* in South America and *Monopterus* in China and Japan live in marshes or the shallow ditches of rice-fields, and bury themselves in the mud when the water dries up, although they have no accessory organs of respiration: probably they are able to breathe air sufficiently by means of the ordinary gill-chamber, which is large.

Among the coral reefs off the coast of Thursday Island in the Torres Straits between New Guinea and Cape York Mr. Savile Kent studied a curious case of association between a small fish and a large sea-anemone. The anemone is, when fully expanded, at least two feet in diameter across the disc, and the fish lives within its internal or digestive cavity without being digested, and without being injured by the poisonous stinging cells of the anemone's tentacles, although the latter usually close upon and kill other animals which come into contact with them. The species of fish which has this peculiar habit is *Amphiprion percula*, and it belongs to the family Pomacentridæ, a tropical family allied to the wrasses of our own coasts. The fishes of this family are as before mentioned usually brilliantly coloured, and this particular species is of a bright vermillion-red with three broad transverse bands of white. The same habit was described in *Amphiprion percula* and another species *A. bifasciatum* long before the date of Mr. Kent's observations, by Dr. Francis Day, in the Andaman Islands. Mr. Kent suggests that the fish escapes from its enemies by retreating into the cavity of the anemone, where they cannot follow it, and confers in return a benefit on its protector by the fact that its pursuers in their haste come into contact with the anemone's tentacles and are killed and devoured. It is very difficult to understand, however, how the fish can live when the anemone contracts its tentacles and stomach in order to kill and digest its prey, and also how the fish can live within the cavity without causing the anemone to contract and kill it. It is possible that the anemone tolerates the presence of the fish although the contact of any other animal causes it to contract, or on the other hand it may be that the

fish is skilful enough to enter the anemone without touching its tentacles or even the sides of its stomach. The case is so extraordinary that if we did not know it to be true it would seem almost as incredible as the ancient fable of the salamander living in fire. It is not, however, the only case of its kind, for a similar companionship occurs between an allied species of anemone and a prawn, the latter having a brilliant coloration similar to that of the fish.

*Glyphidodon anabantoides*, another of the Pomacentridæ, protects itself by hiding among the branches of corals. Day found at the Andaman Islands that some of these fish could always be captured by obtaining pieces of coral from the bottom of the water: the fish remained closely packed in the crevices of the coral even when it was broken off and brought to the surface by the native divers; fear did not cause them to leave their retreats, but only to penetrate more deeply into them.

Fish are infested with numerous parasites of various kinds, both internal and external, but it rarely happens that non-parasitic fixed growths, whether of animal or vegetable nature, are found on their bodies. Hydroid zoophytes and sea-anemones are frequently found growing on the shells of bivalve molluscs, or on the shells inhabited by hermit-crabs, and in several such cases a particular species of hermit-crab is invariably associated with a particular species of hydroid or anemone. A single case of a similar association between a fish and a hydroid zoophyte has been described by Lieut.-Col. Alcock in his *Naturalist in Indian Seas*, in which he gives an account of the results of the scientific investigations made on board the *Investigator* in the Bay of Bengal. The fish in question, *Minous inermis*, belongs to the Scorpænidæ, most of which are characterised by large heads furnished with formidable spines. Most of the Scorpænidæ are of inactive habits and live on the bottom or among rocks, and many of the species afford striking examples of what is called "protective resemblance"; they have inconspicuous colours in irregular blotches harmonising with the rocks, weeds, stones, etc., and often the skin is abundantly furnished with loose membranous flaps or filaments, which by waving about in the water make the appearance of the fish still more deceptive. In *Minous inermis*, which is only a few inches long, and lives on the east coast of India, the skin is actually covered with living

hydroid zoophytes, and these probably serve to hide it even better than appendages which only resemble natural growths of the sea-bottom. The hydroids are of a species (*Stylactis minoi*) which has been found only on this fish, and the fish has never been found without the hydroid. The zoophytes are not parasitic, they feed by means of their own mouths and tentacles and absorb no nourishment from the fish. The case is therefore one of commensalism, the two organisms probably benefiting one another reciprocally, the hydroid by being carried about from place to place and so getting more food, the fish by being concealed or disguised ; it is possible that the fish is also directly protected, the hydroids being distasteful and inedible. With regard to the origin of this invariable association, it is evident that the hydroid could not grow on the fish unless the latter were very sedentary in its habits, but it is difficult to understand why only one species should grow on it, and not grow elsewhere. A Darwinian would probably hold that a particular variation occurred which could only survive under these peculiar conditions ; a Lamarckian, on the other hand, might suggest that in the course of generations the peculiar mode of life caused changes in the hydroid which made it a distinct species.

Association between young fish and large jelly fishes or medusæ is of common occurrence in European seas. One of the earliest naturalists to notice this was the Norwegian, G. O. Sars, who, when he was investigating the life-history of the cod in 1867, found the young of that species when an inch and a half in length were to be found almost exclusively under the umbrellas of the medusæ, which were very abundant. This observation was made off the Lofoten Islands in the north of Norway. Sars found that the young cod were feeding on the crustacean parasites of the jelly-fish. The young of the scad, *Caranx trachurus*, exhibit the same habit. The young of *Tetragonurus*, a Mediterranean fish belonging to the Percesoces, have been observed to take up their abode in the respiratory cavity of large Salpæ, animals which have the transparency and the mode of life of jelly-fishes, but which are related to the sea-squirts or Ascidiants, and therefore to the Vertebrates.

Another very remarkable case of association between fishes and other animals is that of *Fierasfer* and its allies which live in the bodies of sea-cucumbers or Holothurians (Fig. 24).

*Fierasfer* is a fish of slender shape, from four to seven inches in length; its whole body is very transparent with only traces of pigment in the skin; it has pectoral fins, but no pelvic, the dorsal fin extends from a little behind the head to the posterior extremity, which is tapering and pointed, the anus is near the head and the ventral fin extends from it to the end of the body;



FIG. 24.—*Fierasfer* and Holothurians (after Emery).

there is no tail fin. In an aquarium the fish is observed to seek the anus of the Holothurian with its head and then to bend round the extremity of its tail and insert it into the aperture after which it straightens itself and moves backwards until it has passed completely into the body of its host. Within the latter it is found to be contained within the cavity of one of the tubes which open into the cloaca, and which are known as the

respiratory trees. More than one fish may enter successively into the same Holothurian; in the aquarium at Naples, Prof. Emery saw as many as seven pass into the same animal one after the other; but in Holothurians captured in the sea, never more than three were found together, and when larger numbers entered the host soon died. The fish are only found in Holothurians captured in deep water, those found near shore being always free from them. The entrance of the fish is facilitated by the respiratory movements of the host, which is obliged at intervals to dilate its anal aperture for the expiration and inspiration of water. The fish obtains no food or nourishment from its host, its stomach being always found to contain crustaceans which are not to be obtained from the intestinal cavity of the Holothurian. It seems probable that the fish is in the habit of leaving its host to catch its prey, and that it does this at night, retiring into its living shelter at the approach of daylight, but this has not been observed; all that has been seen is that the Fierasfer sometimes protrudes its head and front part of its body from the anal aperture of the Holothurian; it could scarcely catch crustacea in such a position. In Holothurians captured from the sea the Fierasfer is usually found in the body cavity, into which it can only pass by rupture of the delicate walls of the respiratory tree, but this apparently causes no great harm to the Holothurian. The fish is not, properly speaking, a parasite, since it does not feed on its host, and it is not what is called a "commensal" or messmate, because it appears to confer no benefit on its host, it is merely, as Prof. Emery says, an uninvited guest. Its existence within the Holothurian evidently depends on the peculiar mode of respiration of the latter, the fish obtaining its oxygen from the water inspired by its host. The fish might thus be called a respiratory parasite, but the origin of the habit is merely to be attributed to the instinct of the fish to seek shelter from its enemies in holes and crevices, as do the conger and *Muraena* and many other fishes.

Off the coasts of Japan a species of Fierasfer lives not only in Holothurians but also in the body of globose starfishes of the genus *Culcita*, and on the tropical coast of America *Fierasfer dubius* is found within the valves of the pearl oyster, *Meleagrina margaritifera*, and occasionally the dead body of the fish has been found in the shell entirely enclosed in mother of

pearl. The affinities of *Fierasfer* are somewhat doubtful, formerly they were supposed to be related to Ophidiidæ and Blenniidæ, but from the structure of the skull they seem to be of a more primitive type, and Mr. Boulenger places them in a special division with the deep-sea Halosauridæ and a few other forms.

The sucking fishes of the genera *Echeneis* and *Remora* are provided with a curious sucking disc on the dorsal surface of the head by which they attach themselves to sharks, whales, porpoises, turtles and even occasionally to boats or ships. In a broad sense of the word they may be said to be parasites, but they do not feed on their host; their food consists of other fishes and the advantage of their habit is that it protects them from their enemies and enables them to dart out unexpectedly on prey which they would not be swift enough to pursue by themselves. They may perhaps be regarded as commensals as they probably catch fish which their hosts have pursued for themselves or even devour fragments which escape from their jaws. The sucking disc is a modification of the anterior dorsal fin just as the ventral sucker of the gobies, the lump-sucker, and sucking fish of the family Gobiesocidæ, is formed by the pelvic fins. The second dorsal and anal fins are long, placed near the tail, and symmetrical with each other. It is not very difficult to understand how the habit of these fishes and the structural adaptation arose from the habit common to many fishes of lurking under the shelter of any large object in the water, for the purpose of concealment and ambush. The adhesive power of the sucker is very great, and on the east coast of Africa the maritime natives make use of the fish for the capture of turtles; the Remora is attached to a line by a metal ring passed round the base of the tail and taken to sea in a boat; when a turtle is sighted the fish is put overboard and attaches itself to the animal, which can then be drawn in and captured.

The Remora was formerly supposed to be one of the Scombriform or mackerel-like fishes, but is now placed by Mr. Boulenger in a separate division of the Spiny-finned fishes (Acanthopterygians). The celebrated pilot-fish, *Naukrates ductor*, on the other hand, is placed among the Scombriformes in the family Carangidæ, represented by the common scad or horse-mackerel. It is a rather small fish, about a foot in length,

the dorsal and ventral fins are elongated and nearly symmetrical, each being preceded by a few detached short spiny rays; the colour is bluish above with five or six dark transverse bands. The tail is, as in the mackerel, forked. It is a truly oceanic fish found in the open oceans all over the world in warmer latitudes. It is common in the Mediterranean and was well known to the ancients. The habits of this fish have been frequently described by travellers, but most of the accounts are vitiated by the tendency of unscientific observers to attribute human feelings to the lower animals, and no recent scientific observations on the subject are available. That one or several pilots usually accompany large sharks is an undoubted fact, and they also frequently follow sailing ships; the latter habit often brings them in summer to the south coast of England, where several specimens have been captured from time to time. The attraction is probably similar in both cases, namely the supply of food from refuse thrown overboard in the one case, fragments that escape from the shark's meals in the other. There is no evidence that the shark receives any benefit from the pilot, any more than the lion does from the jackal; the pilot swims up to a baited hook thrown out for the shark, and shows great interest in the bait, but instead of warning the shark of the danger, of which he is as ignorant as his big companion, he is evidently eager that the shark shall seize the food, which usually happens, with fatal results to the shark. The account of Dr. Meyen, published in 1834, which is still frequently quoted, suggests that the pilot probably feeds on the shark's excrement, but there is no evidence of this; the stomach has been found full of small fish, but probably the pilot like the shark will eat any sort of animal food.

Among the pelagic fishes of the family Stromateidæ belonging to the Sub-Order Percesoces, habitual association with floating objects has been observed. *Lirus perciformis*, which has been named the rudder-fish, a short deep-bodied fish with a rounded snout living in the temperate North Atlantic, especially on the American side, has the habit of taking up its abode within floating barrels, or broken boxes, or of following floating logs. The attraction in this case seems to be the barnacles with which floating timber is usually covered. In 1901 a large shoal of this species followed a floating log which was stranded at the Aran

Islands off the west coast of Ireland. The log was covered with barnacles on which the fish, of which there were several hundreds, were feeding. The islanders were so frightened at the strange fish, which they declared were sheogues or fairies, that they all ran away, and an old man who took some home for eating was not allowed to take them into his house. Another species, *Lirus medusophagus*, has received its specific name, meaning "feeding on jelly-fish," from the fact that at least when young it is constantly found sheltering, like the young of our own Gadidæ, under large medusæ in the open ocean, but it is not known to feed on such animals. Another species of the family, *Nameus gronovii*, distinguished by its very large pelvic fins, has been observed in New South Wales to live habitually beneath the Portuguese man-of-war, *Physalia*, as many as ten specimens of the fish being found under one of the *Physalia*, and when the latter are driven ashore the fish are often stranded with them. It has been suggested in this case that the fish is unaffected by the poison of the tentacles of the *Physalia* and that it feeds on the animals killed by the jelly-fish. *Nameus* is only about three inches long.

Parasitism is rare in fishes. The curious habit of the little Siluroid *Vandellia cirrosa*, can scarcely be called parasitism, as it is only accidentally and occasionally exercised. This fish is only 6 cms. or  $2\frac{1}{5}$  in. in length, and only about an eighth of an inch in diameter; it is believed by the natives of the banks of the Amazon to enter the urethra of men bathing, being attracted by the urine, and it is said that when it has once entered it cannot be pulled out again because of the spines on its opercula. Whether the belief is well founded or not, it is certain that the natives protect themselves from the fish by wearing, when bathing, a special shield formed of a small perforated cocoanut shell.

True parasitism is exhibited by another small Siluroid, namely, *Stegophilus insidiosus*, which lives in the gill-cavity of large species of the same family, especially *Platystoma coruscans* which grows to a length of six feet; the parasite and its host are also South American fresh-water fishes. In this case the parasite sucks blood from the gills of its host.

External differences between male and female are less conspicuous in fishes than in mammals and birds, but are neverthe-

less, of frequent occurrence and of great interest. Among characters peculiar to the males the following kinds may be distinguished : (1) organs directly concerned in the fertilisation of the ova, usually intromittent organs for introducing the milt into the body of the female ; (2) structural peculiarities for aiding the union of the sexes ; (3) weapons used by the males in fighting with one another ; (4) structures which may be displayed in courtship, but which are of the nature of ornaments or appendages, not of mechanical use ; (5) peculiarities of colour.

Intromittent organs in the male are necessarily confined to those fishes in which fertilisation is internal. They are universal in Elasmobranchs (sharks, dog-fishes and skates) and Chimaeroids in both of which sub-classes they consist of outgrowths of the posterior parts of the pelvic fins and have been incorrectly called claspers. In the dog-fish, *Scyllium canicula*, each of these organs has a deep groove on the posterior and internal surface leading to a deep glandular pit at the base of the organ ; in copulation the two grooves are placed together, both organs are inserted into the cloaca of the female and the seminal secretion is conducted along the grooves. Among the skates (Raiidæ) there are other differences between the sexes besides the claspers. In some species the teeth are different ; in the common thornback, for example, the teeth of the adult male are pointed and sharp, there are about forty transverse rows in each jaw and the outer teeth are lozenge-shaped, the central ones conical with the points turned inwards. In the female the teeth are flat and smooth, arranged in oblique rows, the central being larger than the lateral. In the young males the teeth are flat as in the females. In the males of all the species there is an area of large sharp spines on the dorsal side of each wing or pectoral fin, and this is wanting in the females. These may be used for holding the female or for fighting with other males ; the latter employment seems most probable, as it is difficult to understand how spines in such a position could be used in coition, whereas if the males buffet one another with their wings the spines would be effective weapons. Pennant stated as long ago as 1776 that several males pursue one female.

Male Chimaeroids possess in addition to the intromittent organs, commonly but erroneously called posterior claspers, organs of the second kind used for holding the female. In the

male Chimæra an anterior portion of each pelvic fin is separated from the rest and provided with two large dermal spines. The most peculiar organ, however, is a knobbed process covered with spines situated on the middle of the head a little in front of the eyes. The organ, known as the frontal clasper, is directed forwards and below it is a depression into which it is lowered when not in use. Professor Bashford Dean found on females of *Chimæra colliei* taken off the coast of California, very distinct marks and scratches on the skin at the base of the dorsal fin, and believes that these were caused by the frontal clasper of the male, which probably curls its body about that of the female and inserts the spines of its clasper into her skin in the position described. *Harriotta*, which has been taken in the North Atlantic at depths of 707 to 1081 fathoms, has no frontal clasper, and the posterior claspers are small and rudimentary; it has been suggested that the eggs in this genus are fertilised after extrusion. In *Callorhynchus* of the South Pacific the organs are similar to those of Chimæra.

In the Dipnoi or lung-fishes there is one peculiar character confined to the males in the South American *Lepidosiren*: the pelvic fins are covered in the breeding season with processes of bright red colour from the numerous blood-vessels they contain. The use of these structures is discussed in the section on breeding habits.

In the North American Bow-fin (*Amia*) among the living Holostei the male is distinguished by its smaller size and by a black spot at the base of the caudal fin.

In the male salmon during the breeding season the anterior end of the lower jaw grows into a large hook-like process which is turned vertically upwards and when the jaws are closed occupies a deep cavity between the primaxillary bones of the upper jaw. This process serves as a weapon in the fights of the male salmon, which make violent charges at each other. It is a well-known fact that in fishes the males are usually smaller than the females, and Darwin remarks that as in many kinds of fish the males habitually fight together it is surprising that they have not generally become larger and stronger than the females through the effects of sexual selection. It is probable, however, that in those cases in which the males have the habit of fighting they are really larger than the females. It

is not stated that the male salmon is smaller than the female, the sex of large specimens not being usually given in the records. It is certain that the male of the dragonet (see Plate XXV.), which is remarkable for its activity in courtship and rivalry with other males, though it can scarcely be said to fight, is considerably larger than the female. The same is the case with *Coris julis*, a species of wrasse occurring in the Mediterranean, in which secondary sexual characters are well marked though its sexual habits have not been described ; the male attains a length of sixteen centimetres or six inches while the female does not exceed five inches. In the Scald-fish, *Argoglossus laterna*, also, the males are distinguished by pronounced secondary characters and attain to a larger size than the females. Thus in fishes as in mammals, birds, and other animals, greater size seems to be constantly associated with greater activity on the part of the males in connection with reproduction, whether the activity is shown in actual fighting with rivals or in other results of sexual excitement.

The changes which take place in the males of the species of *Onchorhynchus*, the salmon of the Pacific, at the spawning season are as follow : both jaws become greatly prolonged and hooked, so that either they close by the side of each other like shears, or cannot be closed at all, the front teeth grow to a great length, as much as half an inch, the body grows more compressed and deeper at the shoulders so that a distinct hump is formed, the scales become covered by spongy skin, the colour changes to various shades of black and red according to the species. In the dragonet, *Callionymus lyra*, (Plate XXV.) the male is much larger and the anterior rays of his first dorsal fin are greatly elongated, as well as the second dorsal and the ventral to a less degree ; the sides of the body and head and the surface of the vertical fins are ornamented with alternate bands of bright blue and yellow, while the female is a dull mottled brown. The actions of the male correspond to these peculiarities ; he can scarcely be said to fight, but he rushes about in a state of great excitement, trying to frighten other males, and erecting all his fins and showing off his colours before the females. These antics lead up to an actual pairing, for although in this species fertilisation is external and the eggs are buoyant and free, the male lifts the female by placing his pelvic fin under hers and



MALE AND FEMALE DRAGONEE (*CALLIONYMUS LYRA*) IN PAIRING ATTITUDE. THE MALE IS MUCH LARGER AND MORE BRIGHLY COLOURED THAN THE FEMALE



they swim vertically upwards side by side while shedding the eggs and milt. In the Scald-fish the peculiarity of the male is also the elongation of the anterior dorsal fin-rays and those of the pelvic fin. In *Coris julis* also the male sexual characters are larger size, elongation of fin-rays, and more brilliant coloration.

A very marked difference of coloration occurs in *Labrus mixtus*, one of the British wrasses ; the male is yellow or orange with longitudinal blue stripes, the female is red with three large black spots on the hinder part of the back. Unfortunately the habits of this species in the breeding season have not been observed.

In the majority of the species of the carp family (Cyprinidae) the males develop in the spawning season, hard, wart-like tubercles on the skin, which disappear after that season is over. It has been shown that these nuptial excrescences are used in some species in the battles of the males, or in nest-building, while in some two males hold the female between them, pressing against her and against one another behind and beneath her. In the armoured cat-fishes (Loricariidae) of South America there are also great sexual differences between the sexes, but the habits of these are not so well known, except that they build nests.

Among the toothed carps (Cyprinodontidae) sexual differences are naturally most developed in the viviparous species, since in these the males and females play different parts in the drama of courtship and sexual union. The males in such species are smaller and more brightly coloured and also less numerous. In a few cases there are sexual characters in the males which are not directly connected with copulation ; in *Mollienisia petenensis* the dorsal fin of the male is very greatly enlarged and marked with ocelli, and in *Xiphophorus hellerii* the ventral margin of the caudal fin is developed into a long filament. The copulatory organ is formed by modification of the ventral fin, which consists of few rays and is situated immediately behind the anus and genital aperture. Erich Philippi of Berlin has recently discovered a viviparous species, *Characodon lateralis*, in which the ventral fin of the male is not modified, but is similar to that of the female. In a number of other species such as *Gambusia*, *Mollienisia* and *Xiphophorus*, the ventral fin

of the males is much elongated and provided at the extremity with little finger-like processes, but there is no tube running down the fin from the genital aperture. In two species of *Gladarichthys*, Philippi succeeded, by observations on specimens kept in an aquarium, in discovering how the milt of the male is introduced into the female duct in these cases. It is evident that if the milt was liquid as in ordinary fishes it would be difficult to introduce it without the aid of a tubular intromittent organ. Philippi observed that the male in copulation bent his ventral fin round either to the left or right so that its extremity pointed forward and somewhat to the dorsal side, and then darted at the female, touching the genital aperture with the processes at the extremity of his ventral fin. The contact was only momentary, the impetus of the male carrying him onwards beyond the female. It was impossible to see any milt passing from one fish to the other in this proceeding, and it was evident that the genital apertures of the two fishes were separated by the whole length of the ventral fin of the male. By slight pressure on a male fish lying on a glass slide Philippi found that small lumps of milt were expelled which adhered to whatever they touched. These masses were found to be composed of spermatozoa surrounded by an adhesive liquid, and the testes were full of such masses, which form what in other cases are called spermatophores. It is evident then that some of these spermatophores are ejected at the moment of contact of the ventral fin with the female in the movement above described, and that they are drawn into the female duct by some sucking action. The formation of spermatophores thus prevents the dispersal of the spermatozoa in the water.

In other species, as in *Jenynsia* and the four-eyed fish *Anableps*, a closed tube continued from the genital duct runs down the front of the elongated ventral fin of the male, so that the spermatozoa are conducted directly to the female aperture, and it is not known that spermatophores are formed in these cases. Whether there is a tube on the modified fin or not, copulation takes place sideways, and it is found that in a given fish it always takes place on the same side. In *Anableps* there is a kind of hinge in the middle of the fin on the side of which is a fleshy tubercle. When this tubercle is on the right the fin bends to the left, when it is on the left the bend is to the right. In

the females the genital aperture is covered by a large scale, called a foricula or little shutter, which is attached on one side and open on the other, the opening being to the right in some specimens, to the left in others. Garman found in a number of *Anableps* examined the majority of the males were rights and of the females, lefts; the number of lefts was 35 per cent. in the males, 62 per cent. in the females. We have here, therefore, a case of asymmetry closely similar to that of the flat-fishes: in the one case the asymmetry is related to different relations of the two sides of the body to the external world, in the other to reciprocal relations between the sexes. In the flounder, as in the Cyprinodonts, we find lefts and rights in the same species.

In many fishes, as already mentioned, the males are smaller than the females. This is the case where the male guards the spawn or the nest as in the Lump-sucker so common on the coast of Scotland, where the two sexes are known as cock-paidle and hen-paidle. In the flat-fishes, e.g. sole and plaice, the males are considerably smaller, and in plaice evidence has been recently obtained to show that this is partly due to the fact that the females live to a greater age. The maximum difference seems to be reached in the eel family as more fully described below in the life-history of these fishes. The present writer does not believe that these sexual differences are explained by sexual selection; he has pointed out that the process of selection or survival cannot account for the limitation of the characters to one sex, to the adult age, and often to one period of the year, namely the spawning season, while on the other hand the characters always correspond to external irritations which occur only under the same limitations as the characters. The reasonable conclusion is therefore that the characters have been caused by these irritations, arising from the actions of the males under sexual excitement. The smaller size of the males which guard the spawn or the nest may be explained as due to the more sedentary habits required by such duties, but the cause in other cases such as that of the eels is not so obvious.

## CHAPTER V

### MODES OF REPRODUCTION

Oviparous and viviparous Elasmobranchs ; eggs of Chimæroids. Nests of Protopterus and Lepidosiren. Nest-building of Ganoids and primitive freshwater Teleosteans. Parental instincts in British shore-fishes. Nest of the Sargasso. Fishes which incubate the eggs in the mouth. Pouch of the Pipe-fishes. Viviparous fishes. Curious breeding habits of the Bitterling.

THE sharks, dog-fishes and skates (*Elasmobranchii*) and the Chimæroids (*Holocephali*) possess oviducts which are distinct and separate from the ovaries. Fertilisation is internal, the milt being introduced into the oviducts by means of the copulatory organs which are posterior outgrowths of the pelvic fins. The eggs as they leave the ovaries, are usually of considerable size, and resemble the yolk of a bird's egg. In some species the fish are oviparous, and in these each oviduct contains a special gland which secretes a shell of horny texture and of flattened oblong shape, in which the egg, together with some albuminous secretion, is enclosed ; the egg when laid has thus a structure quite similar to that of a bird's egg, but the shell is of different shape and contains no lime ; it is therefore tough, but not brittle. In the common ground dog-fishes of the genus *Scyllium* the corners of the egg-shell are prolonged into long slender tendrils which are coiled round fixed objects or seaweeds at the bottom of the water, and thus anchor the egg during development. The development occupies several months and the young fish is hatched in a condition resembling that of the parent. In other cases the female is viviparous, the development of the egg taking place within the oviduct, and in some of these species, as for instance in the common spiny dog-fish, *Acanthias vulgaris*, a rudimentary egg-shell is formed around the egg in its early condition ; the young when born are fully developed and able to seek their own food ; seven or eight young are produced at a birth, each of them several inches

in length. Comparatively few of the shark-like fishes (Selachii) in addition to *Scyllium* are known to be oviparous : *Pristiurus*, the black-mouthed dog-fish of the Mediterranean, is one of these ; *Heterodontus* or *Cestracion*, the Port Jackson Shark and allied species of the Australian, Japanese, and Californian coasts, have an egg-shell of very peculiar shape, consisting of an elongated conical capsule with two broad flat flanges winding spirally round it and two long coiled tendrils at the pointed end.

The common skates and rays of the genus *Raia* are also oviparous, the shell being broader than in *Scyllium* and having stiff processes at the corners instead of tendrils.

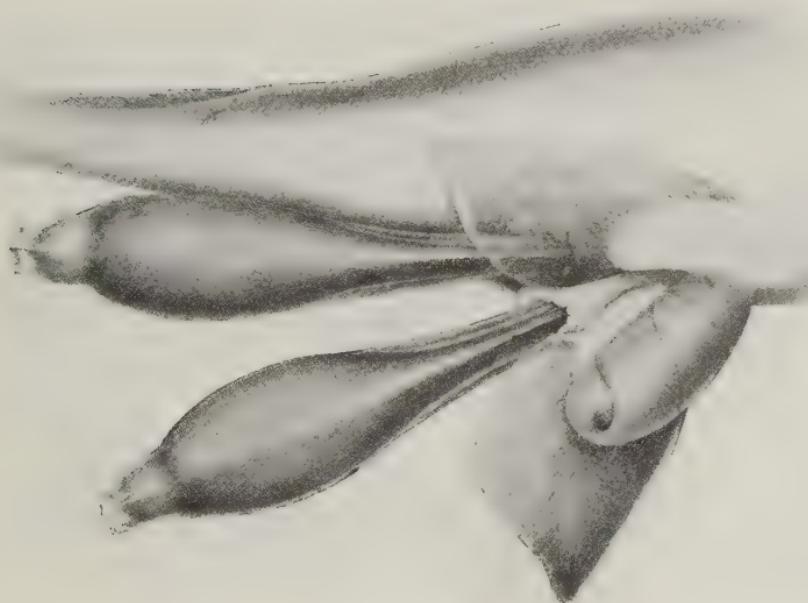
Among the viviparous forms the best known are *Carcharias* to which genus belong most of the large dangerous sharks of tropical seas, *Galeus vulgaris*, the Tope, in one of which were found thirty-two young, *Sphyraea* or *Zygæna*, the curious hammer-headed sharks in which the head is produced on each side into a great outgrowth bearing the eye at its extremity, the Notidanidæ distinguished by having more than five branchial clefts, *Mustelus*, the hounds, one of which occurs in British seas, *Rhina* the monk or angel-fish, the Torpedinidæ or electric rays, the Trygonidæ or sting-rays, and the Myliobatidæ or eagle-rays. Internal development involves the possibility of the nutrition of the embryo by absorption of secretions from the wall of the oviduct, a possibility which renders the provision of yolk of less importance, and which in mammals has led to the disappearance of the yolk and the evolution of a special organ connecting the developing young with the wall of the oviduct, the organ called the placenta. In viviparous Elasmobranchs we find many examples of the evolution of structures adapted to the nutrition of the embryo or foetus : in many species long filaments called villi or " trophonemata " (nourishing threads) are developed from the inner wall of the uterus, and these secrete a nutritive liquid which is absorbed by the embryo either by the blood-vessels of its yolk-sac or by its digestive organs. In *Pteroplatea*, one of the sting-rays of the Indian Ocean, two bundles of such trophonemata pass through the greatly enlarged spiracles of the embryo, and pour their secretion into its stomach. Some species of *Mustelus* and *Carcharias* exhibit a closer similarity to the relation of the embryo to the uterus which is characteristic of mammals : folds or pro-

jections of the vascular wall of the yolk-sac, penetrate into the wall of the uterus and adhere to it, so as to form a true yolk-sac placenta, through which nutrient material diffuses from the maternal blood-vessels into those of the foetus. The existence of this placenta in the smooth dog-fish of the Mediterranean, *Mustelus levis*, was known to Aristotle, but it is a curious fact that in the species which occurs on the British coasts, *Mustelus vulgaris*, no such placenta is formed. One species of the Elasmobranchs is exceptional in its mode of reproduction, namely the Greenland shark, *Læmargus borealis*, the eggs of which are not enclosed in a shell formed by the oviduct and are fertilised after being shed like those of Teleosteans.

All the existing Chimæroids resemble the oviparous Elasmobranchs in the character of their eggs and in the nature and development of the egg-shell. The latter is elongated, and consists of a narrow central portion in which the egg is contained, and a flat flange on each side. (Plate XXVI., A and B.) The cavity of the elongated capsule consists of three portions, the widest portion a little behind the anterior end, elliptical in shape, which contains the yolk of the undeveloped egg, an anterior portion very short in *Chimæra*, and only a little narrower than the first mentioned part, but narrower and longer in *Callorhynchus*, and a posterior portion almost half the length of the whole capsule and very narrow. The anterior portion is the first formed, and is posterior in position when the egg is in the oviduct; when the embryo is developed this part contains the snout. Owing to the close correspondence between the shapes and sizes of these different parts of the egg-capsule and the parts of the young fish which is developed in it, Professor Bashford Dean of New York distinguishes them as snout-sheath, trunk-sheath, and tail-sheath. The capsule is thus adapted in shape, not to the egg as it exists when the capsule is formed, but to the embryo as it afterwards develops. Still more remarkable are the adaptations in the capsule for the admission of water for the respiration of the embryo and for the escape of the latter when it is hatched. Along the sides of the capsule are a series of apertures which are not open when the egg is laid, but by a process of weathering or decay become open in the later stages of development, and allow of a current of water produced by the respiratory movements of the embryo to enter by the anterior apertures and to



EGG-CAPSULE OF *CHIMAERA COLLIEI*, AFTER HATCHING OF EMBRYO:  
LATERAL ASPECT  
SAME, DORSAL ASPECT



TWO CAPSULES PROTRUDING FROM OVIDUCTS OF FEMALE *CHIMAERA*  
(AFTER BASHFORD DEAN)



escape by the posterior. The dorsal and ventral walls of the capsule are united in the new-laid egg by a membrane, which gradually weakens until at hatching it gives way, and the anterior lips of the capsule spring apart, and leave an opening through which the young fish makes its exit. Professor Bashford Dean has argued that this adaptation of the capsule in several minute particulars to the needs of an embryo which will not exist till long after the capsule is formed is evidence of evolution in a determinate direction, and cannot be explained either on Lamarckian principles, that is by the direct action of conditions, or on the principle of selection. The embryo could not affect the shape or structure of the capsule directly, since the capsule is formed first, and the young fish which was selected by the conditions of its life would not necessarily be the one which had a spontaneous variation to the right kind of capsule. There are, however, considerations which Professor Dean has overlooked. He makes too much of the adaptation in shape, since in other cases, as in the bird and the Teleostean fish, we know that the egg-shell is not in the least adapted to the shape of the embryo, which is packed away inside it in the most complicated distortions. Then again it is possible that the shape of the capsule may have determined to some extent the shape of the fish by its effect on the embryo, as for instance on the tail, supposing that the tail was of little importance to the free life of the fish after hatching, so that it might retain the shape to which it was forced by the egg-shell. On the other hand, the elongated body of the young snake, and the broad flat fins of the embryo of a skate or ray, have to be coiled up in an egg-shell whose shape shows no correspondence whatever with that of the young animal which is hatched from it. It is illogical, therefore, to conclude that the egg-shell of the Chimæroid alone is precisely adapted to the shape of the animal subsequently developed in it, and then to inquire how this adaptation was evolved. It is more reasonable to assume that in all cases the shape of the egg-shell is determined, as in birds and reptiles, by the mechanical and physiological conditions existing in the oviduct, and has no relation to the form of the embryo. In fact the prolongation of the shell of Chimæra into a narrow tube with flat flanges along its edges can be explained satisfactorily by the manner in which the egg is laid.

The expulsion takes place very slowly, for the simple reason that the egg has in the water no tendency to fall out under the action of gravity, and since the secretory activity of the oviduct, which may be considered to be excited by the presence of the egg, diminishes gradually while the empty oviduct is collapsed and thrown into folds, the secreted substance of the shell is necessarily moulded to the cavity of the folded duct. The secreted substance may, must indeed, be regarded as a plastic substance which is being drawn through the folded oviduct by the pressure of the water on the thicker portion of the shell which has already escaped. Professor Dean describes a specimen in which the capsules were protruding: the posterior narrow parts were still inserted in the oviducts and showed no tendency to become detached. (Plate XXVI., C.) He admits also that considerable time is taken in the process of egg-laying. Similar conditions obtain in the case of oviparous Elasmobranchs, and the filaments in the egg-shell of *Scylium* can be explained in a similar way, at least the posterior ones which are the last formed. The female *Scylium* rubs her cloacal aperture against upright objects at the bottom of the sea and the lower tendrils which protrude first having become entangled pull first the egg itself and then the upper tendrils from the oviduct; the latter are therefore pulled out from the secreted plastic substance like a drawn wire. The same reasoning cannot, it is true, be applied to the tendrils which are first formed since they are completed before the main part of the shell is formed, but the effect on the oviduct of the pulling out of the egg may well have influenced its mode of action and shape at the beginning of the secretion of the next egg. Thus instead of saying that the tendrils are adapted to the future attachment of the egg after it is laid, we may conclude that the action of the female in trying to rid herself of the eggs has directly caused the development of the tendrils. At any rate one explanation is as reasonable as the other, unless it can be proved that conditions have no permanent or hereditary effect, and this has not yet been proved.

No other fishes except the Elasmobranchs are provided with a gland in the oviduct which secretes a true egg-shell. The eggs when laid are therefore enclosed only by membranes secreted in the ovary; they are usually small and spherical and

the surface of the membrane may be smooth and hard or adhesive or provided with long filaments.

Of the three surviving genera of lung-fishes (Dipnoi) *Ceratodus* lays its eggs separately and singly among the water-weeds and takes no care of them. This fish lives only in the Burnett and Mary rivers of Queensland, and these rivers never entirely dry up, although in the hot season they are reduced to a series of stagnant water-holes connected by shallow channels where the water has almost disappeared. *Protopterus* lives in the shallow swamps of West Africa, and passes the dry season in holes in the mud, the fish being enveloped in a cocoon formed of hardened mucus secreted by its skin. This aestivation takes the place of the hibernation of our common Amphibia, the latter being due to the winter cold while the former is the result of heat and drought. In both cases reproduction follows the period of torpor. When the swamp has been again flooded by the rains after the dry season *Protopterus* makes near the bank a nest consisting of a hole in the mud about a foot in depth, filled with water and surrounded by the long grasses. It is probably the male which makes the nest, for he remains in the hole guarding the eggs which are deposited by the female on the bare mud at the bottom. Like other male fishes which exhibit parental instincts the male *Protopterus* protects the eggs from two kinds of danger, that of being devoured by other animals and that of death from want of oxygen. He bites viciously at any living creature which intrudes into the nest and he keeps the water aerated by lashing movements of his tail. The South American *Lepidosiren* has somewhat similar habits, our knowledge of which is due chiefly to Professor Graham Kerr who made two expeditions to the Chaco Boreal, west of the upper part of the River Paraguay, for the purpose of investigating the breeding and development of this lung-fish. *Lepidosiren*, like *Protopterus*, breeds at the beginning of the rainy season, making for its nest a new burrow distinct from that in which it aestivates. The nest-burrow differs from that of *Protopterus* in being much longer and in the fact that it consists of two portions, a vertical portion extending about a foot from the surface and a horizontal part from a foot to four feet in length. At the end of this burrow the eggs, which are similar to those of Amphibia, are laid by the female, and as in the case of *Protopterus* the male

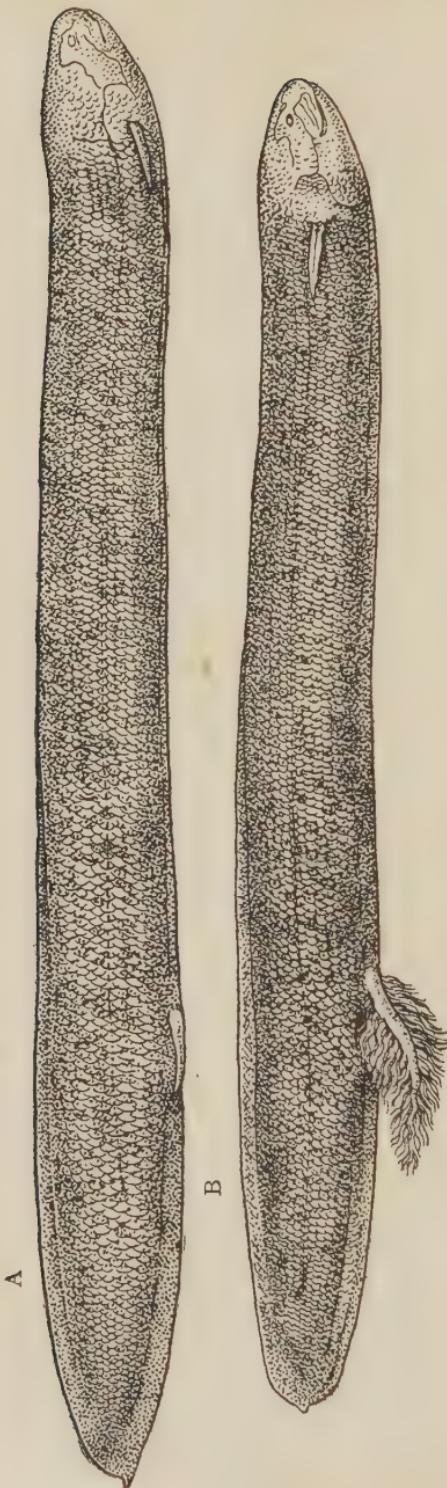


FIG. 25.—South American Lung-fish (*Lepidosiren paradoxa*). A, female; B, male.

remains to guard them. During this time the slender cylindrical hind-limbs of the male are enlarged and covered with close-set blood-red filaments two or three inches in length (Fig. 25, B). These structures afford an interesting example of secondary sexual characters in the male which disappear after the breeding season. Evidently they have some definite function in relation to the care of the eggs. It has been suggested that they act as accessory gills, enabling the male to obtain sufficient oxygen without leaving the burrow to inspire air at the surface. Considering, however, the function performed by the male *Protopterus* and by other male fishes which guard their eggs, of providing the latter with oxygen during their development, it would seem more probable that the use of the filaments in *Lepidosiren* is to provide for the respiration, not of the parent himself, but of the ova. The water in the burrow is probably deficient in oxygen, and the eggs may be able to

absorb this gas from the vascular filaments which are perhaps in contact with them.

The habits of the North American bony-pike, *Lepidosteus*, in the spawning season were described by Mr. S. W. Garman in 1878 from observations made at Black Lake, Ogdensburg, in the State of New York. The lake is connected with the river St. Lawrence. Although there are many *Lepidosteus* in the lake they are seldom seen except in the spawning season, between 15th May and 8th June, remaining at other times in deep water. The eggs are deposited on irregular heaps of granite fragments which form the extremities of small promontories projecting from the shore. The temperature was 68° to 69°F. Usually a female swam to and fro with a male against each side with his beak reaching toward the back of her head. After moving slowly to and fro for some time the fish would suddenly lash about violently scattering eggs and milt. The eggs were adhesive and attached themselves with great tenacity to the rocks. The males are much smaller than the females, the largest of the latter sex taken was 4 ft. 1½ in. long. On 31st March multitudes were seen in all places of the character described, they remained only two days. When they were in the shallow water the fish were seen to rise frequently to the surface and take a gulp of air, opening the mouth widely and closing it with a snap. The eggs were 5 mm. in diameter.

One species of bow-fin, *Amia calva*, is extremely common in the lakes and rivers of the Eastern States of North America, for example in Lake Erie, the lakes of New York State, and in South Carolina. It exhibits distinct sexual differences, the male, as is usual in fishes, being considerably smaller than the female; the latter may attain a length of four feet and a weight of thirty pounds while the male is only about two-thirds as large, more slender and lighter in proportion. In April and May the mature fish come from the deep water to the reedy shallows to spawn. The ova are deposited in definite nests made by the removal and beating down of the rushes over a circular space, so that the sunlight shines directly on the ova. When preparing the nest the fish actually bite off rushes which they wish to remove and even floating fragments are carried away so that the surface above the nest is kept clear. The spawning parties are stated to consist of a single female accompanied by several

males, but others have observed only a single male to be present. The latter account of the matter is easier to understand since only a single male remains to tend the nest and eggs after they are fertilised. The number of eggs in a nest vary from a few hundreds to several thousands, but it is not known whether they are always the product of a single female or of several. A passage through the reeds provides access to the nest, and the male remains on guard either in this passage or in the open water of the nest itself; sometimes he remains for hours without motion except the movements of the lateral fins and those

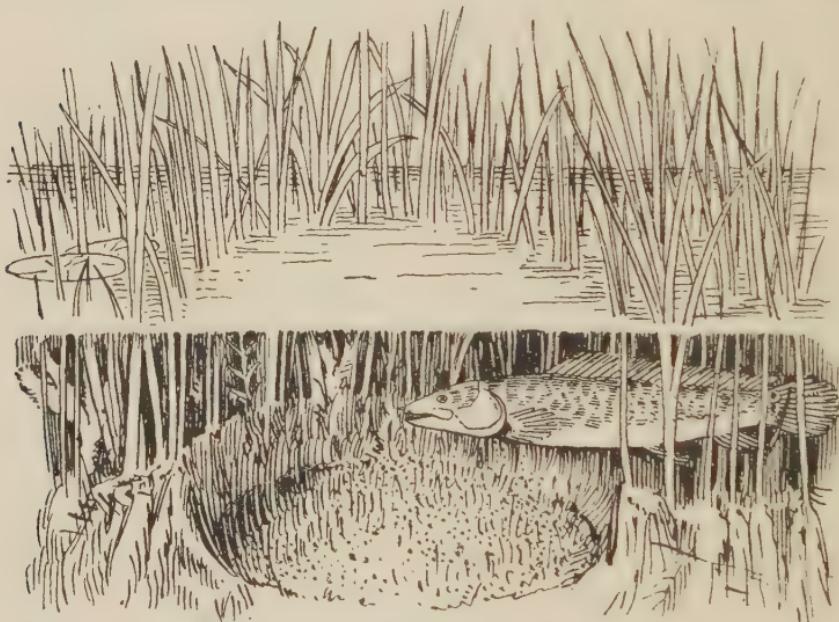


FIG. 26.—Nest of American Bow-fin (*Amia calva*) after Bashford Dean.

of respiration, at other times he is more restless; he frequently by vigorous respiration produces currents of water over the eggs and thus supplies them with oxygen. The depth of water in the nest varies from a few inches to three or four feet (Fig. 26). The eggs are hatched after eight or ten days and then the male parent continues to take care of the larvae which remain with him in a more or less compact swarm. For the first few days the larvae remain inactive in the nest attached to fragments at the bottom by their sucking discs. The young fish continue to follow the male for several weeks and in one case Mr. Summer in Minnesota observed a swarm of young which were three to four

inches in length and about four months old still attended by the father. The following description of the habits of the male when in a charge of a swarm of young is given by Bashford Dean from direct observation: "In a slow and cautious way he circles about, now over and now under his swarming charges, watchful apparently that the stragglers shall keep up to the rest; and in their turn the young fish seem to fully realise that it is their duty to keep as close as possible to their guardian. It was found by no means easy to approach the male fish without attracting his notice; he appears to be constantly watchful and when alarmed exhibits the greatest solicitude for his charges. Sometimes he backs quietly into some reed-screened pool, hiding below in the shadow of floating weeds, his presence only betrayed by the black mass of larvæ about him; at other times he will sulk cautiously away, drawing the swarm after him as rapidly as possible. His duty is clearly to care for his charges and when he finds it impossible to carry them off with him, he will in the majority of cases remain quietly and face the enemy. In one instance he was actually pushed away. There can be no question that the feeling of alarm of the guardian may be transmitted to the young, for in case of need the swarm can be moved more rapidly, the young, excited in their movements, appearing to draw more closely together; under all circumstances they appear to be careful not to disperse. When the male has been driven away the swarm sometimes becomes so dense that it may be taken almost to a fish by a single dip of the scap-net; if not interfered with it will gradually move away and take refuge among the floating weeds often so perfectly that no trace of it can be noticed."

Several of the tropical fishes of the primitive families Mormyridæ and Osteoglossidæ, build remarkable nests which have been described by the late J. S. Budgett, a young Cambridge zoologist, whose premature and much-regretted death was directly due to disease contracted on his scientific expeditions to the swamps of West and Central Africa. *Gymnarchus*, one of the Mormyridæ which has a long dorsal fin, but neither pelvic, anal, nor caudal fins, makes a floating nest of grasses. The whole nest is about two feet long by a foot broad. Three of its sides project above the surface of the water, the fourth side is about two inches, and the bottom about six inches below the

surface. The whole nest is thus somewhat like the ark of bulrushes which served as a cradle to the infant Moses. In this nest are deposited about a thousand amber-coloured eggs, a fifth of an inch in diameter, which hatch in five days. After about eighteen days the fry leave the nest, they are then three inches long. The construction of the nest was not observed, nor was a parent fish found guarding it, but Budgett was informed by the natives that the parent is usually present and defends the nest with formidable bites. This nest was studied in the swamps of McCarthy Island in the river Gambia and in the same swamps were found the enormous nests of *Heterotis*, the African genus of the Osteoglossidæ. These nests are four feet in diameter enclosed by walls eight inches thick made of the grasses removed from the interior while the bottom is the smooth bare ground of the swamp. They have the appearance of miniature lagoons among the dense aquatic vegetation. The eggs of the fish, which are about a tenth of an inch in diameter, cover the bottom of the nest and hatch in two days. *Sarcodaces odoe*, an African species of the Characiniidæ, lays in the same swamps its eggs in a floating foam formed of some secretion enclosing bubbles of air and when the larvæ are hatched they hang for some time from the surface of the water by means of a large sucker-like organ on the front of the head.

Many of the cat-fishes (Siluridæ) make some sort of nest and take care of their eggs. The common horned pout, *Amiurus nebulosus*, of North America, and other species of the genus, deposit their eggs in holes under logs or in old pails or other receptacles thrown into the water, or in holes excavated in the mud. Both parents co-operate in the preparation of the nest, but only the male remains to guard the eggs, and he leads the young when they are hatched in large shoals near the shore. *Doras* and *Callichthys* of the same family in South America build nests of grass or leaves, sometimes placed in holes in the bank of the river. The Loricariidæ have similar habits. Many of the Centrarchidæ, the common sun-fishes of the United States, are known to build nests. The gourami, *Oosphromenus*, and the paradise fish, *Macropodus viridi-auratus*, readily breed in aquaria, the male constructing a nest of air-bubbles blown with a secretion from the mouth and watching over eggs and young.



SPAWN OF LAMPSUCKER (*CYCLOPTERUS LUMPUS*)



EGGS OF GAR-FISH (*RHAMPHISTOMA BELONE*) ATTACHED TO SEAWEED



BUTTER-FISH GUARDING ITS CLUMP OF SPAWN



Parental instincts are exhibited by several of the shore fishes which are common on the British coasts. One of the most frequently observed cases is that of the Lump-sucker (*Cyclopterus lumpus*), whose spawn is attached in large masses in crevices of the rocks above the level of low water at spring tides. The individual eggs are rather large varying from 2·2 to 2·5 millimetres in diameter, the average being therefore about one-tenth of an inch, while the clumps of spawn are sometimes of extraordinary size, measuring as much as a foot in length, eight inches in breadth and three or four inches in thickness. It is not certain however that a mass of such large size is the product of a single female. The fresh-laid spawn is more or less brightly coloured, the tint being often a distinct bluish-red or a delicate pink, in other cases it varies from dark to light yellow. The surface of the egg-clumps is not uniform but is broken by large conical depressions which allow the water to penetrate into the interior of the mass; these pits are made by the male which presses his head into the mass when it is first deposited before the adhesive secretion which holds the eggs together has hardened. (Plate XXVII., A.) The effect of this action is twofold; it presses the spawn firmly into the crevice of the rock and gives it a firm attachment, and it prevents the eggs being crowded together too closely so that the central ones would be suffocated. The male parent fertilises the eggs at the time of their extrusion by the female, and then remains near them and guards them with constant care until they are hatched. He removes any animals such as starfishes, crabs, or molluscs, which crawl on to the spawn and fearlessly defends his charge against any enemies, such as other fishes, which threaten to devour it. Dr. Ehrenbaum, who studied the habits of the fish on the shores of Heligoland, where it is very abundant, states that he saw a male bite the finger of a fisherman who tried to take the spawn out of an aquarium, so severely as to draw blood. From time to time the male which is guarding a mass of spawn, pushes his head into one of the depressions which have been described above and sends a powerful stream of water through the mass by a reversal of his respiratory movements. It appears therefore that the successful hatching of the majority of the eggs is due to this artificial method adopted by the male parent for supplying them with oxygen, and that the natural movements of the

water would not be sufficient for the respiration of such a dense mass of large eggs. Ehrenbaum states that the male when guarding a mass of spawn in this way, attached by his ventral sucker to the rock, when excited throws his whole body into a peculiar trembling vibration and produces a loud and distinct sound resembling the rumbling of distant thunder. The spawning period of the lump-sucker is from January to April, principally in February and March.

The butter-fish (*Centronotus* or *Pholis gunnellus*), has been observed by Mr. Holt and others to roll its clump of spawn into a ball by twisting its body round it, both parents taking part in this proceeding. (Plate XXVII., C.) It seems certain that one of the parents remains coiled round the spawn and guarding it, but it has not been decided whether only the male or both parents perform this duty. Professor M'Intosh of St. Andrews states that he found the clumps of spawn with one of the adult fishes in the holes bored in the rocks by the boring bivalve Mollusc *Pholas*. Ehrenbaum found that in the neighbourhood of Heligoland the spawn was always found between the valves of empty oyster-shells accompanied by one of the parents.

The male parent in the case of the common sand-goby (*Gobius minutus*) makes a simple nest by scooping out the sand from beneath an empty scallop-shell. The female deposits her adhesive eggs on the lower surface of the shell which forms the roof of the nest, and the male remains in the latter supplying the eggs with a constant current of water by the action of his pectoral fins.

The nest-building habits of the common stickleback are widely known and are easily observed. In this case also it is the male parent alone which shows any solicitude for the welfare of his offspring. He makes a nest by collecting together the vegetable rubbish which is found at the bottom of the stagnant fresh waters in which he lives, and arranging it in the form of a round heap with a depression at the top, like a bird's nest. He then seeks a female and goes through a process of courtship the result of which is that she accompanies him to the nest and deposits her eggs in it. Several females may spawn in the same nest but they are all fertilised by the male to which it belongs, and he continues to guard it till the eggs





NEST OF SEA-STICKLEBACK (*GASTEROSTEUS SPINACHIA*) WITH CLUMP  
OF SPAWN IN THE CENTRE. THE FRONDS OF WEED ARE BOUND  
TOGETHER BY A THREAD SPUN BY THE FISH  
(AFTER EHRENBAUM)

are hatched, driving away intruders and fighting fiercely with other males if they come too near.

The marine stickleback, *Gastrostomus spinachia*, which is common on British shores and is much larger than the fresh-water species, reaching a length of six to eight inches, not only builds a nest but binds the materials of it together with a thread spun from its own body. The nest consists of growing sea-weeds, and the kidneys of the male in the breeding season secrete a gelatinous substance which hardens as it is drawn out into a strong white continuous fibre, and this is wound about and woven into the nest as the fish swims about it during its construction. (Plate XXVIII.) This fish, therefore, may be said to spin a cocoon somewhat in the same manner as a silkworm or other caterpillar or a spider; the silk of the caterpillar or spider however is secreted by special glands while in the fish the secretion comes from the kidneys; there are differences also in the use made of the secreted fibre, the caterpillar makes a cocoon only to protect itself in the pupa stage, or as an aid to locomotion, spiders very generally spin cocoons to contain their eggs, but many of them also spin webs and snares for the capture of prey. The sea stickleback affords the only instance of spinning among the vertebrates of which we have certain knowledge. Among the floating masses of the sargasso weed in the Sargasso Sea, that is to say in the middle of the North Atlantic, occurs frequently a fish-nest which at first sight seems to be constructed in the same way as the nest of the fifteen-spined stickleback. This nest consists of fronds of the weed held together by threads and containing clusters of fish-eggs, but careful examination has shown that the threads in this case are processes or outgrowths of the egg-membranes, two bundles of them arising from each egg at opposite poles of its surface. The threads must therefore be produced, as in the eggs of the gar-fish, *Belone acus* or *Rhamphistoma belone* (Plate XXVII., B), and some other species, in the ovary during the development of the eggs. The nest has been shown to be formed of a single plant of the sargasso weed, which is allied to the common *Fucus* or bladder-wrack of our own coasts, and like it has air-bladders in its fronds which cause it to float. All the complicated ramifications of the plant are drawn together by the threads so that the nest has a spherical form and is about twice as large

as a human fist, in other words it is about six inches in diameter. Many of these nests were taken and examined during the voyage of the French exploring vessel "Talisman" in 1883. They have also been described by the American naturalist Alexander Agassiz, who died recently after a long and distinguished career. Until lately the nests in question were generally attributed by naturalists who had studied them to the sargasso-fish, scientifically known as *Pterophryne*, a small fish allied to the well-known angler or fishing frog of our own seas. This fish belongs to a family most of whose members live among coral-reefs, where they are concealed by their colour and the appendages of the skin; but *Pterophryne* makes use of the peculiar arm-like pectoral fins which are characteristic of all the angler tribe, to support itself on the floating sargasso. Recently, however, an American naturalist Mr. Gudger, has had the opportunity of observing the spawning of *Pterophryne* in the aquarium of a Biological Laboratory in S. Carolina. Specimens of the fish were living in a tank with pieces of sargasso weed, and when they spawned they made no nest at all, and produced eggs not provided with threads but held together in a sheet of gelatinous material exactly like the spawn of the common angler. The nests found in the sargasso must therefore be the work of some other, at present unknown fish, and it is most probable that this unknown parent is one of the flying fishes, since these belong to the same family (Scombresocidæ) as the gar-fish (*Belone*), the eggs (Plate XXVII., B) of which are known to be provided with filaments arising in groups from opposite poles.

The curious habit of carrying the eggs in the mouth during their development occurs in two families of fishes widely separated in classification, namely the cat-fishes (Siluridæ) and the Cichlidæ, the former belonging to the primitive sub-order of carp-like fishes (Ostariophysi) and the latter to the most specialised group of Teleostei, namely the perch-like fishes of the spiny-finned group. In their general appearance and structure the Cichlidæ, formerly called by Günther Chromides, resemble the wrasses of our own coasts, and as previously suggested may be regarded almost as fresh-water wrasses. It is difficult to account for the evolution of such a habit; we can only form conjectures concerning the modes in which it might have arisen. If we assume that it was throughout due to

paternal solicitude, we may suppose that the parent fish watched over its eggs and took them into its mouth to remove them to a place of security, and then gradually developed the habit of retaining them till they were hatched. On the other hand it is not impossible that the habit owed its first origin to a very different intention on the part of the parent; it is known that many fishes eat the spawn of other fish and also their own when they have the opportunity, and some of the eggs taken into the mouth to be eaten may have escaped being swallowed and remained in recesses of the pharynx till they were hatched. We have seen that one of the most important conditions for development is a constant supply of oxygen, and this condition could be nowhere better fulfilled than in the pharynx of the parent, through which water is constantly passing in the normal respiration of the fish. As the two families are so remote it is obvious that the habit must have been developed in each independently, and they do not resemble each other closely in mode of life: only a few species of cat-fishes have the habit, and these are marine and estuarine, while it is common to all the Cichlidæ and they live exclusively in fresh water.

The Cat-fishes which have adopted this mode of protecting their eggs are species of *Arius*, *Osteogeniosus* and *Galeichthys*. *Arius* is cosmopolitan, species occurring in Asia, Africa, America and Australia, but the habit is not followed by all the species, *Arius australis*, for example, has been observed by Dr. Semon to form nests in the Burnett River in Queensland. These nests consist of circular excavations about twenty inches in diameter in the sandy bed of the river; the eggs are deposited at the bottom of the hole and are covered over by several layers of large stones. According to the well-known ichthyologist Francis Day who was at one time Inspector-General of Fisheries in India, all the Indian species of *Arius* carry their eggs in their mouths; the eggs fill the cavity of the mouth as far back as the gills, and he never found any food in the stomach or intestines of fish carrying eggs in this way, so that during the incubation the males are evidently unable to feed. *Arius commersonii* is a large species occurring in South America, it reaches three or four feet in length, and is the most commercially important fish of the Rio Grande; in the language of Brazil it is known as the bagre; it is dried for use as food, its bladder

is used for isinglass, its oil for tanning. It spawns in November, December, and January, and according to von Jhering comes from the ocean to the river for this purpose. The eggs are large, measuring 18 mm. or nearly  $\frac{3}{4}$  in. in diameter, and males with eggs in the mouth do not take the hook, which indicates that they take no food while in this condition. In 1857, Dr. Wyman investigated this mouth-gestation in several species of Siluroids at Paramaribo in Dutch Guiana; the species belonged to the genus *Bagrus* or one nearly allied to it. His account contains some particulars in addition to those given above. The mouth and branchial cavity were very much distended by the eggs which were twenty to thirty in number, the gill-cover being round and swollen. Dr. Wyman observed that the hatched larva or foetus found in the mouth in some cases weighed more than the undeveloped egg, and concluded that it had grown at the expense of some other nutriment than that derived from the yolk, so that there is some possibility that the eggs are not merely protected in the mouth cavity but also absorb nutriment from its secretions. *Galeichthys* is an African genus, and Mr. Boulenger received a specimen from Port Elizabeth with thirty eggs in its mouth, but does not say whether the sex was male or female.

Species of Cichlidæ are found in Asia, Africa, and America, but are absent from Australia. In some species it is stated that the male carries the eggs, in others the female, but Mr. Boulenger states that in the African species it is certainly the female only which carries out the incubation, all specimens with eggs in the mouth being of this sex. In some cases at least the parent not only incubates the eggs in its mouth but also guards the young after hatching, and receives them into its mouth again when any danger threatens them. Thus Dr. Reinhold Hensel, writing of observations in South Brazil in 1870 and referring to a species called *Geophagus scymnophilus*, states that in December the summer was too far advanced for him to see the spawning process, but he frequently had opportunities of observing the parent with a brood of young; he says the parent was probably the male but did not ascertain this with certainty. In a shallow part of the stream near the bank a shoal of 20 to 30 young swim about while the old fish keeps watch at some little distance. When alarmed the old fish swims to the shoal of

young and they collect together around his mouth as though at the word of command, then they disappear within the mouth cavity and he swims quickly away. The author was unable to catch the old fish with the young in its mouth by means of a net, but obtained one specimen in this condition by shooting it in the water; the young were closely crowded together with their heads directed backwards towards the gills. It is a very widespread and ancient belief that the young of the viper seek refuge from danger in their mother's mouth and stomach. Spenser in the "Færie Queen" in describing Error under the form of "a monster vile," half-woman and half-serpent, evidently thought he was adding a characteristic quite natural to a serpent when in reference to her young ones he wrote the lines:—

Soone as that uncouth light upon them shone,  
Into her mouth they crept, and suddain all were gone.

It is curious that science has entirely failed to obtain any confirmation of this popular belief, which must be considered to be entirely without foundation so far as the viper or any reptile is concerned, and on the other hand it is an ascertained fact that at least one kind of fish not only hatches its eggs in its mouth but takes its young into the same cavity when they require protection.

In *Aspredo* a genus found in South America, and closely allied to the Siluridæ, the eggs after fertilisation become attached to the skin of the ventral surface of the female, each egg being borne by a little stalked cup connected with the skin. In the males of the pipe-fishes (*Syngnathidæ*) the eggs are carried by the male during development either in a ventral pouch behind the anus, as in the sea-horse *Hippocampus* and the common British pipe-fishes *Siphonostoma* and *Syngnathus*, or attached to the skin of the abdomen as in *Nerophis*. In *Solenostoma* of the Indian Ocean it is the female which carries the eggs in a brood-pouch formed by the pelvic fins.

Viviparous reproduction occurs in several families of Teleostei, namely the Cyprinodontidæ, Embiotocidæ, Scorpaenidæ, Comephoridæ, Blenniidæ and Zoarcidæ. Of these only the first belongs to the more primitive Teleosteans with open air-bladder, being placed in the sub-order Haplomi, whose best known representative is the pike. The Cyprinodonts,

whose name means literally toothed carps, are confined to fresh or brackish waters. The other four families are all members of the most modern or specialised sub-order of spiny-finned fishes (*Acanthopterygii*), and with the exception of the *Comephoridae* are all marine. In the Californian surf-perches (*Embiotocidae*) the physiological peculiarity is common to the whole family, but in *Comephoridae*, *Scorpænidæ*, and *Blenniidæ* it is confined to a few species in each family. It is difficult therefore to attribute the viviparous habit to the same conditions of life in all cases, it appears to be in a sense accidental, although it has doubtless arisen from an intensification of the sexual instinct of the male which led him to an increasingly definite psychological interest in the spawning of the female. In many fishes, as we have seen, the males show a very distinct interest in the process of fecundation and a strong association between their perceptions of the female and of the eggs, and their own sexual excitement. The nervous connection in such cases is no longer merely between the enlarged and mature sexual organs and the act of expulsion of the contents of the latter, still less is there a merely automatic escape of the milt, but the discharge is the response to stimulation of the brain by the higher sense-organs. Such stimulation and psychological excitement has led the male gradually to anticipate the discharge of the eggs by the female until the milt was actually introduced into the female aperture. Once internal fertilisation has taken place, the explanation of internal development offers little difficulty.

It seems evident that such a development of the sexual instinct could only occur in fishes of comparatively sedentary habits, and under favourable conditions of life, in which food was abundant and the persecution of enemies not very severe. The Cyprinodonts are small fishes of which the largest do not exceed a foot in length, and occur chiefly in the rivers and fresh waters of the American continent, in the southern parts of North America, in Central America, and in South America as far south as La Plata. A few species are known from tropical and subtropical regions of the Old World, namely Africa, India, Arabia, and the East Indies. They are represented in the more southern islands of Japan, and also in southern Europe, namely in Spain, Italy and the Balkan peninsula. The *Embiotocidae* or surf-perches are confined to the north Pacific and

are especially characteristic of the coasts of California, but some are also found on the shores of Japan. They are small fishes, short and deep in shape of body, and allied to the Labridæ or wrasses of our coasts. It is a remarkable fact that viviparous fishes are more abundant on the Pacific coast of North America than anywhere else in the world, no less than 30 per cent. of the fishes of this region, according to Eigenmann, exhibiting this mode of reproduction. In addition to numerous species of Embiotocidæ, there are many belonging to the genus *Sebastodes*, one of the Scorpænidæ, to which family belongs also the European viviparous form *Sebastes norvegicus*. This last species is an inhabitant of the northern Atlantic: it occurs at depths ranging to 100 fathoms along the west coasts of Sweden and Norway, in the White Sea, off the coasts of Nova Zembla, Spitzbergen, Iceland, Greenland and Newfoundland, and along the American coast as far south as Cape Cod. Many other species of *Sebastes* are known, but only *norvegicus* is viviparous. This species has occasionally been taken on British coasts, chiefly in Scotland, but in some cases it has been confounded with another species, *Scorpæna dactyloptera*, which is not viviparous. Of the Blenniidæ, in the restricted extent now given to the family, only one genus is viviparous, namely *Clinus*, of which several species occur off the coast of South Africa. The so-called viviparous blenny of British and European coasts, *Zoarces viviparus*, is now placed in the separate family Zoarcidæ, allied to the Blennies. Of this family three other genera are known to be viviparous, one of these being the Cuban cave-fish *Lucifuga*. These cave-fishes of Cuba, *Lucifuga* and *Stygicola* are the only members of the family which live in fresh water. It is curious that the cave fishes of Cuba and those of Kentucky, although belonging to widely remote families, should be alike viviparous.

In viviparous fishes, as in other animals whose young develop within the body of the mother, the two points of chief interest are the modes in which, firstly, the nutrition and, secondly, the respiration of the developing embryos are effected. It is obvious that as the embryo has no direct contact with the external medium, oxygen must be obtained from the maternal supplies. There is on the other hand no immediate necessity for a change in the mode of nutrition. Embryos which develop

externally are nourished by the yolk contained in the egg, and when development takes place within the ovary this mode of nutrition is not necessarily altered. It becomes, however, possible for the embryo to absorb nourishment from the secretions of the ovarian walls or from the maternal blood-vessels, and thus the supply afforded by the yolk may be supplemented or the amount of yolk may be diminished and the new supply of nourishment may be to a greater or less degree substituted for the old. Among the Cyprinodonts the gestation has been chiefly studied in *Gambusia* and *Fundulus*, two North American genera, and in *Anableps*, the curious South American form whose eyes are divided into two halves, one for seeing things above and the other things below the surface of the water. It must be remembered that the ovaries of Teleosteans are usually closed sacs, the inner surface of which produces the eggs, each originally enclosed in a separate cavity, called the follicle, in the ovarian tissue. *Gambusia patruelis* is a species living in the fresh waters of Virginia. The adult males are only  $1\frac{1}{2}$  in. long, the females  $1\frac{3}{4}$  in. The ovaries are united into a single sac and at each gestation twenty to twenty-five yellowish eggs are produced. The eggs do not leave the follicular sacs in which they are developed; these follicles, instead of bursting as in ordinary cases and liberating the eggs into the cavity of the ovary, merely form a small opening in their walls and through this opening sperms enter and fertilise the egg which goes on developing within the follicle. In this species the wall of the ovarian sac has disappeared and the follicles are exposed to the body cavity, the young escaping at birth by an abdominal pore. Another peculiarity is that the egg is not provided with an egg-membrane, although in the allied genus, *Fundulus*, this structure is present. An egg-membrane is not essential to an egg that develops within its follicle, and thus we can understand why it has disappeared in *Gambusia*. The walls of the follicle are richly supplied with blood-vessels, and the developing fish obtains its oxygen from the maternal blood within these, but although the follicle contains liquid around the embryo this does not appear to contribute to the nourishment of the latter, for the yolk is not exhausted till the young fish is completely developed and ready for birth, when its fins and fin-rays are completely formed, and it resembles its parent

in all respects except size. The young fish at birth is  $\frac{1}{2}$  in. long.

In *Anableps* Wyman found that the number of embryos varied from four to eighteen in a single female. The ovaries were united into a single sac into which the follicles containing the embryos projected. In this species the yolk was soon absorbed, and after the first stages the umbilical sac contained no yolk, although it was of large size; it was occupied by coils of the intestine. The external surface of the sac was covered with a number of parallel series of projecting processes which followed the course of the blood-vessels in the wall of the sac. Evidently here we have a more modified condition than in *Gambusia*: the embryo is no longer nourished entirely by the yolk but the papillæ on the walls of the sac have been evolved for the purpose of absorbing nourishment from the follicles; the latter contain a nutritious liquid secreted by their walls, which are richly supplied with blood-vessels. This adaptation is closely similar to that which is found in *Mustelus* among the Elasmobranchs and to what is called the yolk-sac placenta in mammals. In one specimen of *Anableps* were found seven embryos  $2\frac{1}{4}$  in. in length whose development was nearly completed; the yolk-sac had disappeared and was only represented by a thin membrane on the lower side of the abdomen, on which no trace of the absorbing papillæ of the earlier stages remained. The embryos or young fish had escaped from the follicular sacs and were lying free in the cavity of the ovary; evidently they were almost ready for birth. In these embryos of various stages of development could be traced in a most interesting way the gradual development of the extraordinary horizontal division of the eyes which is peculiar to *Anableps*: in the youngest embryos the eyes were simple as in ordinary fishes, in later stages the iris developed lateral projections, and finally the cornea was divided by a horizontal band. The details and the significance of this modification of the eye are discussed in another part of this volume.

The Embiotocidæ belong to the division Perciformes of the Acanthopterygii, and accordingly in general characters they are not unlike the common perch. They have a single elongated dorsal fin, of which the anterior part is spiny, the posterior soft or flexible. It is a curious fact that although copulation

has not been actually observed in these fishes it is known to take place several months before the eggs are fertilised, namely in June or early July. After this time the ovary of the adult female contains a quantity of milt, and the eggs mature and are fertilised between the beginning of November and the end of January, those of the larger and older individuals maturing earlier. The mature eggs are of extremely small size in comparison with those of other fishes, being only .2 millimetre, or  $\frac{1}{12\frac{1}{5}}$ th of an inch in diameter. This reduction in size is due, as in the case of the eggs of mammals, to the almost entire absence of yolk, the embryo being supplied with nourishment from the ovary after development has commenced. The egg is fertilised while still within the follicle, but immediately afterwards it becomes free and lies in the cavity of the ovary. The duration of gestation is about five months and the number of young in a single female varies in *Cymatogaster aggregatus* from three to twenty according to the size of the mother; in other species there may be from twenty to thirty young in one female. The two ovaries are united into one sac, and from the dorsal wall of the sac project several longitudinal folds of membrane, which are richly furnished with blood-vessels and extend among the embryos, supplying them with oxygen and material for their nourishment. At first absorption is effected by the general surface of the embryo, then when the intestine is developed the ovarian secretion is taken into it and digested. Long before the mouth is developed the first pair of gill-slits is opened and the food current enters through these in consequence of the movement of minute processes, technically called cilia, which are developed on the walls of the gullet. At a later stage when the mouth is opened the hind-gut becomes enormously enlarged, and on its inner surface are developed very long absorptive processes or villi which are special adaptations for the absorption of the ovarian secretion. There is also a special adaptation in the later stages for the respiration of the embryo: when the fins are developed their membranes are extended beyond the extremities of the fin-rays and are supplied with a close network of blood-vessels by which oxygen is absorbed from the maternal blood and carbon dioxide given out. The development of these respiratory membranes corresponds to that of the scales on the sides of the body; when the scales are

developed the skin is no longer capable of performing respiratory functions, the rapid interchange of gases through it is no longer possible, and therefore this function is transferred to the delicate fin-membranes which bear no scales and which are enlarged for the purpose. It is curious that in this case the required result is not attained by the elongation of the gill-filaments as it is in the embryo of dog-fishes and in the *Gymnarchus* of the Nile and Gambia. The young of *Cymatogaster* when born are a little less than  $1\frac{1}{2}$  in. in length, the maternal fish being from 7 in. to a foot. In larger species the new-born young may be from 2 to 3 in. long. They are completely developed in all respects except size, the whole of the development being passed through in the ovary, and at the time of birth the special adaptations of intestine and fin-membranes which have been mentioned have entirely disappeared. As in other cases the structural adaptations of embryonic life last only so long as the conditions which render them necessary.

The reproduction of the Scorpænidæ has not been so completely investigated. The Scandinavian naturalists merely state that the young of *Sebastes norvegicus* are born in April or May or even later. The American zoologist Ryder examined a gravid specimen taken off the Banks of Newfoundland in July. He estimated that there were at least a thousand embryos in each ovary, for here the ovaries are not united. These embryos were in an advanced stage of development, though some were still surrounded by the egg membrane, others were free in the ovary. They were slender and only about six millimetres or little more than  $\frac{1}{8}$  in. long. The yolk-mass was large in proportion to the size of the embryo and contained a large yellowish oil-globule. The ovary had very thin inferior and lateral walls somewhat coloured by dark pigment. The dorsal wall was thick and vascular, and from it vascular processes, divided into slender finger-like branches, dipped down among the mass of embryos. It seems clear therefore that in this case the embryo is nourished by its own yolk, and only depends on the maternal tissues for its supply of oxygen which it derives from the vascular ovarian processes just mentioned. The adult *Sebastes* is from a foot to two feet in length. Several species of *Sebastodes* were studied by Eigenmann at San Diego in California. According to his description the eggs are one

millimetre in diameter, that is about the size of many eggs which develop in the sea; the follicles are ruptured before fertilisation takes place, the embryos hatch, that is to say burst the egg-membrane, about a month after fertilisation, but are retained some time longer within the ovary, so that the whole time of gestation is somewhat less than two months. Fertilisation took place in the middle of September and earlier, hatching from the middle of October onwards. The young are much smaller and less advanced in development at the time of birth than in the two families previously considered; in fact although the fins have begun to develop, they are still "larvæ" similar to those of oviparous fishes soon after hatching. In *Sebastodes lœvis*, the largest of the species of this genus, reaching a weight of 30 lbs., Eigenmann estimates the number of embryos in the ovaries at several thousands.

The Comephoridae include only four species, three of which live in deep water in Lakes Michigan, Ontario, and Lake Baikal; the fourth species is marine and occurs on the Pacific coast of North America. *Comephorus* lives in the greatest depths of Lake Baikal; it is colourless but its eyes are very large. It migrates to shallow water in order to give birth to its young and appears to die after this process, numbers being found dead near the shores of the lake.

Of the four viviparous genera belonging to the Zoarcidae, *Zoarces viviparus* is the only species whose gestation has been carefully studied, and our knowledge even in the case of this common fish is far from complete. Copulation has been observed by one author at the end of March, while the present writer found specimens with young ready for birth on the shores of the Firth of Forth in February and March. It would seem from this that the gestation lasts for a whole year, but it is possible that the season of copulation lasts for a great part of the summer and that birth may take place in some specimens earlier than February. It is not known whether fertilisation of the ova takes place immediately after the introduction of spermatozoa into the ovary, or whether as in the Californian surf-perches an interval elapses between the two events. The eggs appear to be fertilised after they have escaped from the follicles. *Zoarces* belongs to the group of shore fishes whose eggs are rather large with much yolk and usually adhesive,

while *Sebastes* has eggs resembling those of open-sea fishes which are small, numerous, with little yolk, and usually buoyant. The egg of *Zoarces* is 2·5 millimetres in diameter. The number of eggs in a single female varies with the size of the mother but is always much smaller than in *Sebastes* and its allies; females of seven or eight inches in length produce from twenty to forty young at a birth, those of eight to ten inches from fifty to one hundred and fifty, while larger specimens have been found to contain three hundred young or even more. The period of development within the vitelline membrane was found by Van Bambeke in Belgium to be about three weeks: he found eggs in the ovary in very early stages of development on the 11th September, and the first hatched embryos on 27th September. It is of course impossible to observe in viviparous fishes the course of development on the same eggs, since a single observation involves the death of the mother and consequently of the eggs also. The fact however that eggs were only beginning to develop in September indicates either that copulation takes place then as well as in spring or that fertilisation does not occur until some time after copulation. The embryo, according to Bambeke, remains in the ovary for a considerable time after hatching, the total duration of gestation being about four months. The young at birth are 1½ in. to 2 in. in length and are fully developed. There can be little doubt that the embryo derives nourishment from the ovary in addition to that supplied by the yolk, but no special adaptations for nutrition or respiration have been described.

The numerous species of the carp family produce adhesive eggs which are attached to aquatic weeds, but they take no care of them. One species of this family has very curious breeding habits. It is a little fish called in Germany the bitterling from its bitter taste (*Rhodeus amarus*). It is only two to three inches long when full grown, and has large smooth scales. The female is provided with a long tube extending from the genital opening, which serves as an ovipositor, and by means of this the fish introduces the eggs into the cavity within the shell of the fresh-water mussels (*Anodon* and *Unio*). In this cavity, where they are well protected from enemies, the ova undergo their development. The respiratory current of water of the mussel provides oxygen for the ova. The eggs are fertilised by the

male after deposition, and it is a most curious case of adaptation of sexual instincts that the male is sexually excited, not by the presence of the female of his own species, but by the sight of the mussel in which the eggs have been deposited.

The spawning habits of the salmon have been already mentioned in connection with their migration. Other fishes, that is the great majority of the species in the class, whether they produce adhesive eggs like the perch and other fresh-water fishes, and the herring, or transparent buoyant eggs like most marine fishes, show no parental instincts but leave the eggs to develop without protection.

## CHAPTER VI

### LIFE HISTORIES

Life-histories of Teleostomi. Eggs of Clupeidæ. Metamorphoses of Angler and Pleuronectidæ. Growth and Maturity. Diseases and Parasites. Life-history of Eels.

THE Elasmobranchs, or fishes of the shark type, and Chimæroids when hatched or born have already acquired the characters of the adult, and this is approximately true of the new-born young of the viviparous species among bony fishes. But in those of the Teleostomi which are hatched from eggs, the young are more or less different from the adults, and have to undergo various changes of structure and habits before they reach the adult condition. The changes may be greater or less in degree and may be more gradual or more abrupt in development in different types. The young stage of an animal when thus distinctly different from the adult is called a larva, and the development of the larva into the adult form is its metamorphosis. The most familiar examples of metamorphosis are those of the tadpole into the frog and of the caterpillar into the moth or butterfly, and in some bony fishes the change is as remarkable in its own way as it is in these two cases.

In all ordinary cases the metamorphosis is gradual and consists chiefly in the development of the fins and fin-rays and of the scales and internal skeleton.

In the hatched larva there is usually a continuous membrane along the median line of the back, round the tail, and along the ventral edge as far as the anus or even some distance in front of the latter ; the paired fins are also simple membranes. The larva of the lung-fishes (*Dipnoi*) is somewhat like a tadpole ; in the Australian *Ceratodus* there are no external gills, but in the African *Protopterus* and the South American *Lepidosiren* there are four pairs of feathery outgrowths quite similar to

the external gills of the young tadpole, projecting freely from the gill-arches, and in *Protopterus* vestiges of these gills are retained throughout life; in *Lepidosiren* they disappear during the metamorphosis. The larvae of these two genera have also, like the young tadpole, a glandular organ of adhesion behind the mouth. The eggs of the surviving fringe-finned Ganoid *Polypterus* have not been discovered; like *Protopterus* it breeds in the rainy season, and Budgett obtained a single larva from the river Gambia. This larva was about an inch long with fin-rays already developed, and had on each side a long feather-like external gill on the hyoid arch.

The eggs of the sturgeons are extremely small in comparison with the size of the adult fish; in the common sturgeon the diameter is only  $\frac{1}{10}$  in. One of the most interesting facts about the development of the sturgeon is that the larva is provided with teeth, although the adult is toothless.

In the larvae of the American bony-pike (*Lepidosteus*) and bow-fin (*Amia*) there are no external gills, such structures being evidently not required in fishes hatched in a more temperate climate and more aerated water than that of the African tropics, where the more primitive forms above mentioned breed. In both *Amia* and *Lepidosteus* the eggs are adhesive, and the larvae are also provided with an adhesive organ, in this case situated not behind the mouth as in the Dipnoi, but at the end of the snout.

Among the Teleostei three kinds of eggs can be distinguished with respect to the properties of the vitelline membrane and the conditions under which they undergo development; first, eggs of which the egg-membrane is hard and smooth and the eggs themselves sink to the bottom like those of the Salmonidae and shads, second, those in which the membrane is adhesive as in the herring and lump-sucker and most littoral fishes, third, those in which the membrane is non-adhesive and the whole egg is very transparent and floats in the sea, as in the great majority of marine fishes. The majority of fresh-water fishes produce eggs which are attached to fixed objects by the surface of the enclosing membrane; this is the case with the perch, whose spawn is attached to water-weeds in comparatively still water. In some cases the membrane is provided with long filaments arising from it in two groups at opposite poles as in the

gar-fish and the flying-fishes. In the smelt (*Osmerus*) which belongs to the salmon family, and which spawns in estuaries, the egg becomes attached to solid objects such as the gravel bottom, or harbour piles and piers, by an outer adhesive membrane. This membrane separates from the inner membrane and becomes turned back, remaining attached to its central part, much as the rind of an orange may be turned back without being completely detached. Ehrenbaum, who studied the development of the smelt in the Elbe, found that large numbers of the eggs became free and drifted to and fro with the tide among the rubbish at the bottom of the water. In a few species of fish the eggs are united together in a transparent gelatinous mass which floats near the surface, as in the angler and in *Fierasfer*. The sheet of spawn of the angler has been frequently obtained off the south coast of England and off the east coast of the United States; it is usually from twenty-five to thirty feet in length, and eighteen inches to three feet in breadth. The spawn of *Fierasfer* forms little transparent cylindrical masses two to three inches long.

The spawning conditions of the Clupeidæ are interesting from the fact that the various species present a complete transition from the usual fresh-water condition to that which obtains generally in marine fishes. The shads, *Clupea alosa* and *C. finta* are anadromous, ascending rivers to spawn in the brackish or nearly fresh water of estuaries. The eggs of these species are free and separate, and simply lie loose at the bottom of the water. The eggs of the herring are adhesive, and become firmly attached to any fixed objects in the water they happen to fall on. Herring shoals spawn at various distances from the shore, and the few spawning grounds which are known from actual investigation are visited annually with great regularity. The eggs adhere to one another and to other objects in small clumps or layers. The ground where the spawn is deposited is usually rough, consisting of coarse gravel, and at a depth of ten to twenty fathoms, or in some cases more. In the Baltic herrings ascend the rivers and in the Schlei the spawn has been found attached to fresh-water plants. The sprat, on the other hand, the pilchard (or sardine), and the anchovy all produce "pelagic ova," that is to say ova which float separately in sea-water, and undergo development in this condition.

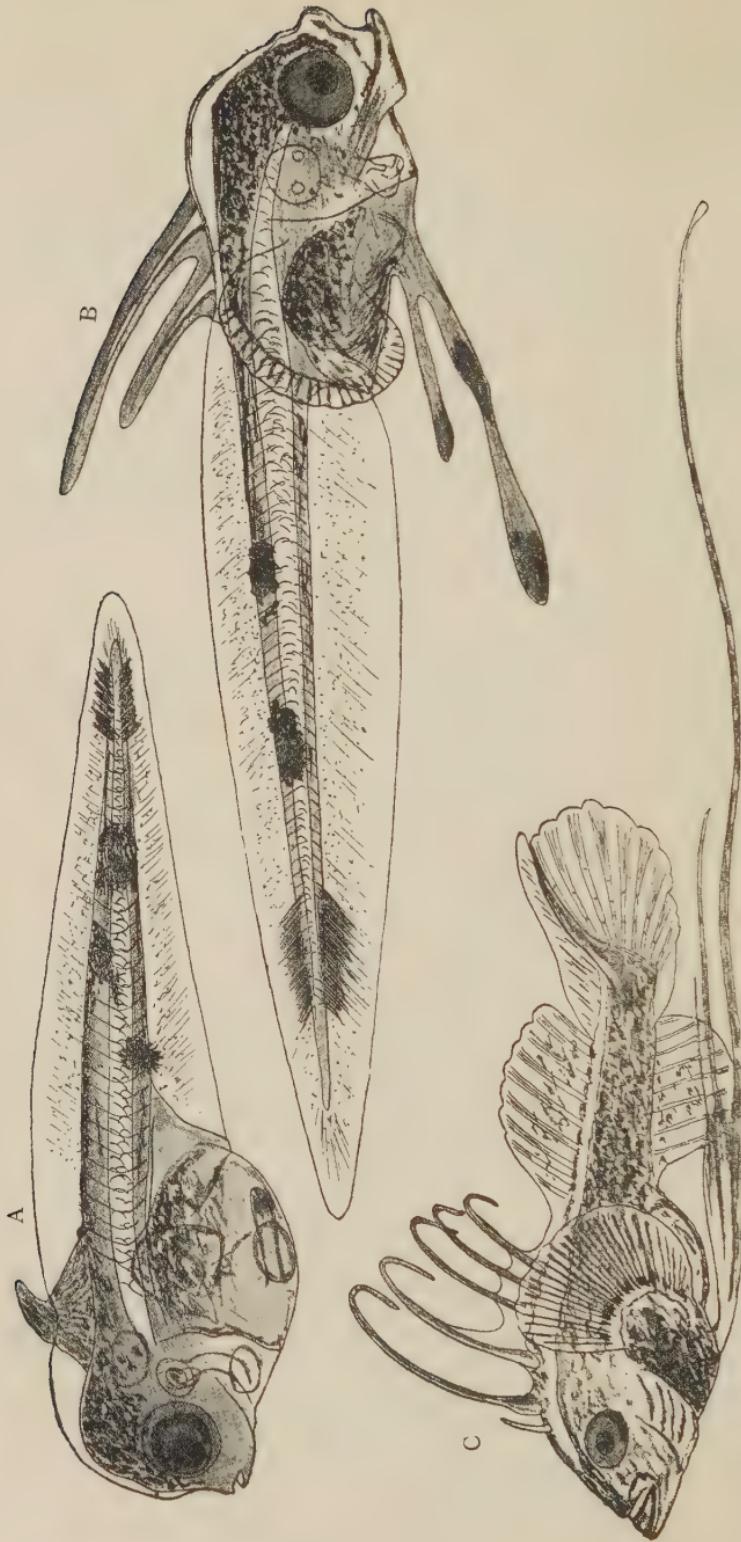


FIG. 27.—Three stages in the metamorphosis of the Angler, *Lophius piscatorius*. A, newly hatched, B, some days old, C, with fin-rays developed.

The eggs of Teleosteans are always small but some are larger than others; the largest are found among those which are heavier than the water, the smallest among those which are pelagic. Those of *Gymnarchus* one of the African soft-finned Mormyridæ are 10 millimetres in diameter, and some of those of the cat-fishes (Siluridæ) which carry them in their mouths are as large as this; those of the salmon are about 5 millimetres. The largest of the eggs of marine fishes are those of the cat-fish *Anarrhichas lupus*, one of the Blennies, which develop at the bottom in deep water; these are 6 millimetres in diameter (a millimetre, denoted by mm., is  $\frac{1}{25}$  in.). The larger the eggs the more advanced in development are the larvæ at the time of hatching; in pelagic eggs the larva when hatched is often without pigment in the eyes, and the mouth is not open. In some cases, as in the angler, the larva is provided with long appendages, formed usually by the elongation of certain fin-rays, and these appendages disappear in the adult. (Fig. 27.) In this case the difference between the larval stages and the adult is very great in consequence of the corresponding difference in habits, the larva being pelagic and the adult living a sedentary life on the bottom. The most extraordinary metamorphosis among all fishes is that of the Pleuronectidæ. In these the larva is similar to those of thousands of other species hatched from pelagic eggs and is perfectly symmetrical, always swimming upright in the water and having an eye on each side, and also pigment on both sides. (Fig. 28, A, B.) As the fin-rays and skeleton develop the eye of one side changes its position and passes first to the edge of the head, and finally to the opposite side, so that both eyes are on one side as in the adult (Fig. 28, C, D). In some species the upper side, possessing eyes and colour, is the right as in plaice, flounder and sole, in others it is the left as in brill and turbot. At the same time the colour disappears from the lower side and the dorsal fin extends forwards towards the end of the snout. The transformation is completed while the fish is still very small; in the plaice and flounder the completely transformed young fish is about  $\frac{1}{2}$  in. to  $\frac{3}{4}$  in. long; the turbot and brill reach a length of one inch or more before their metamorphosis is complete, and they may be often seen at that size swimming at the surface in harbours. In one form of larva originally called *Plagusia* but now known to belong to the

genus *Platophrys* which is allied to the turbot, the eye of the right side seems to come through the head in order to reach the left side. This larva is taken in the open Atlantic in

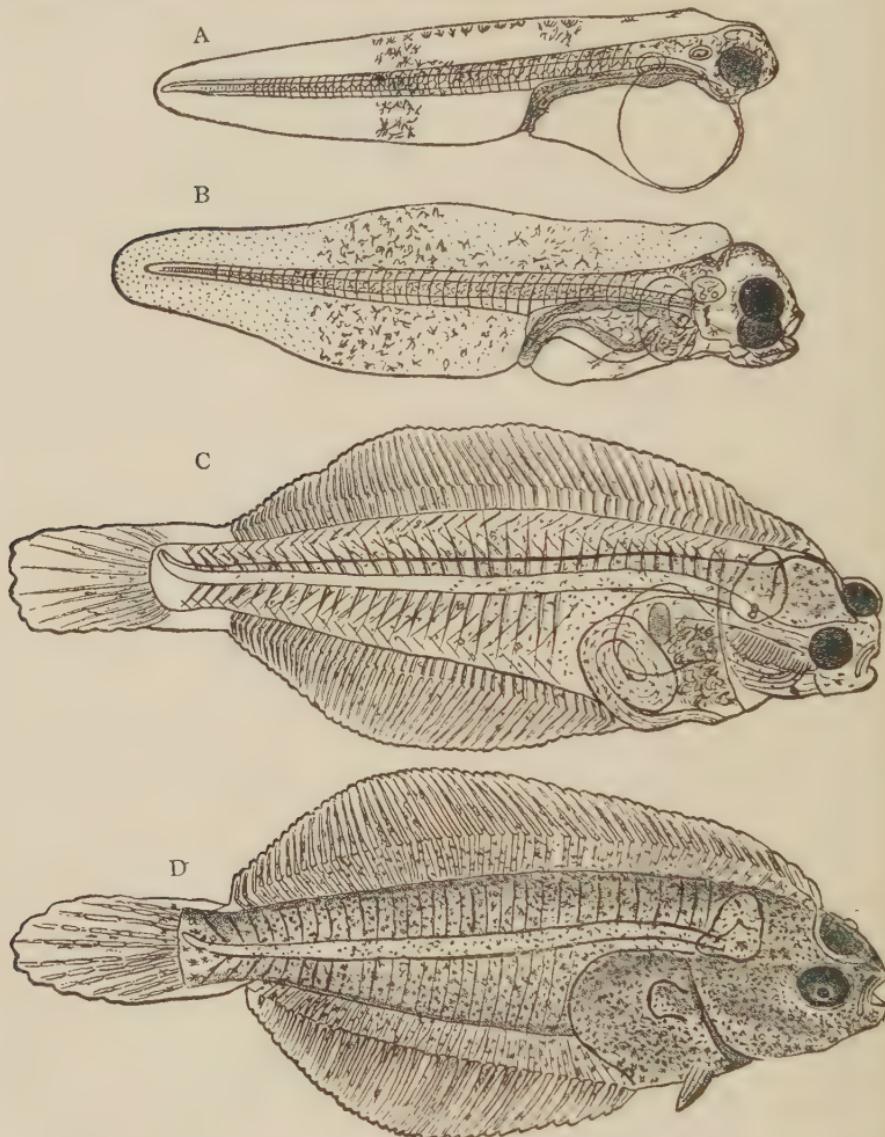


FIG. 28.—Four stages in the metamorphosis of the Flounder, *Pleuronectes flesus*.

southern latitudes and is very transparent; similar forms have been taken in the Mediterranean. The explanation of the difference is that in this form the order of the changes in different organs is altered, that is to say the extension of the

dorsal fin forwards takes place before the eye has migrated. Consequently the migrating eye has to pass under the anterior extension of the fin, although its relation to the skull structures is really the same as in other species. In all cases the apparent movement of the eye is due to the distortion of the skull, the two sides of which develop unequally; the bones between the two eyes are the same as in other fishes and the posterior part of the skull remains symmetrical. The development of the flat-fish is an excellent example of the recapitulation in the history of the individual of the evolution of the race; but it must be observed that the larval flat-fish does not represent the adult ancestor but its larval form; when the adult structures are developed the fish is already asymmetrical.

Until recently the growth of fishes was little understood, but in the scientific investigation of fishery problems a good deal of light has been obtained on such questions as the size and age at which the more valuable food-fishes become mature. This applies specially to the plaice and some other flat-fishes. Fishes do not all become mature at the same size in a given species and the question of size was first attacked by ascertaining that of the smallest mature and the largest immature; thus the limits for female plaice in the North Sea are from thirteen to seventeen inches. The sizes for males are considerably lower. With regard to age there are various methods of investigating the problem. By keeping specimens in aquaria the age can be ascertained; for example, the present writer showed that some flounders became mature at two years, others at three and four years. The results obtained by experiment however do not necessarily apply to fish in a state of nature. One method which has been used with some success for fishes such as plaice captured from the sea is to measure a great many specimens, when it is found that the largest numbers are grouped round certain sizes while there are comparatively few of intermediate sizes; the specimens thus fall into groups which evidently correspond to the produce of successive annual spawnings, and thus the rate of growth and the age and size at maturity are ascertained. More recently it has been found possible in many cases to ascertain the age of a fish by marks in its own structure, as mentioned below in the case of the eel. This method was first invented by a German investigator in the case of the scales

of the carp. It has been shown for the plaice and cod and some other fishes that the otoliths give more distinct indications than the scales. The otolith is a concretion of carbonate of lime formed in the vesicle of the auditory organ ; the deposit formed in summer is opaque while that formed in the latter part of the year is more transparent so that each double zone of white and transparent substance represents one year of age. By this method it has been found that in the plaice the males not only become mature at least a year earlier than the females but die at an earlier age, all the specimens above six or seven years of age being females. Some few fishes appear to be annual, emerging from the egg, attaining maturity and dying within one year ; this is stated to be the case for *Crystallogobius nillsoni* which occurs in abundance at depths between twenty and thirty fathoms off the south coast of England and the south and west of Ireland.

#### LIFE-HISTORY OF EELS

The natural history of the eel possesses a special interest and deserves separate consideration. It is remarkable that the reproduction of so common an animal should have remained an inexplicable mystery from the time of Aristotle until the last few years. And while professional naturalists were until lately unable to trace out the life-history, imaginary explanations of its origin were invented. Aristotle stated that eels arose from  $\gamma\eta\varsigma \acute{\epsilon}\nu\tau\epsilon\rho\alpha$ , literally meaning the entrails of the earth, but the term has been explained as meaning simply earthworms, while the band-like larvae known as Leptocephali, now known to be the young stages of eels, are known to the fishermen of Palermo as *lombrici* or *vermicelli di mare*, worms of the sea. It is therefore suggested that the marine larvae of the eel were not unknown to Aristotle, but it is evident that the chain of reasoning on which the suggestion depends is exceedingly slender, and is not worth serious consideration. At Catania the Leptocephali are called *morenelle*, which means little Murænas.

The family of eels contains a large number of genera and species inhabiting the sea and fresh waters in different parts of the globe. In this country only two species are common, the fresh-water eel and the marine conger. In adult specimens of either species, the generative organs are usually very incon-

spicuous on dissection. The microscope shows, however, that large specimens are invariably female. The characteristic young ova can easily be recognised, but they are embedded in a large amount of fatty tissue, and this fact together with the small size of the ovary, is the reason why the organs were for some time not identified. The ovaries occupy the same position as in other fishes, having the form of a longitudinal band attached to the dorsal wall of the body cavity on each side of the intestine. They differ however from the ovaries of the majority of Teleostei in the fact that they do not form closed sacs with the germinal tissue internal; the germinal tissue in which the ova are developed forms a number of flat folds attached transversely to the outer side of the ribbon-shaped ovary, and exposed to the body cavity. There are no ducts, the ova when shed escaping by pores at the side of the anus.

The male organs are like those of other bony fishes, being somewhat thick, soft, elongated organs, smooth on the external surface, and containing branched microscopic tubes which communicate with a duct leading to the exterior of the body. The male organs of the eel were first discovered by Syrski at Trieste in 1874, but none in the ripe condition were seen by him. Dr. Jacoby in 1877 at Trieste and Comacchio showed that the males were much smaller than the females. The largest male was not quite 1 ft. 8 in. in length, while the female reached a length of 3 ft. 3 in.

In the conger also the male is much smaller than the female. The first description of the ripe male conger is that of Dr. Hermes published in 1881. This naturalist was at that time Director of the Berlin Aquarium, and a number of small conger 2 ft. to 2 ft. 4 in. in length were put into the Aquarium in the autumn of 1879. All of these grew rapidly except one which died in June 1880, and was then only 2 ft.  $5\frac{1}{10}$  in. long. This specimen was found to contain large testes, and microscopic examination showed that the milt which flowed from the organs when they were cut was full of ripe spermatozoa in active motion.

That this specimen was by no means exceptional in its small size was proved by the researches of the present writer at the Plymouth Laboratory in 1887-1890. A considerable number of male conger were obtained and kept alive in the Aquarium, and

examination of these and of numerous dead specimens showed that males were always less than  $2\frac{1}{2}$  ft. in length: in fact the largest male obtained measured only 2 ft. 2 in. A ripe specimen was identified on 13th December, 1888, and was kept alive in the Aquarium until 24th June, 1889, when it died, although its milt was still abundant and healthy. This specimen was 18 in. long and during the period mentioned it took no food. It gradually deteriorated in condition; it became thin and emaciated, and its eyes became ulcerated so that it was quite blind and its skin was ulcerated in several places. Several others were kept alive in the ripe condition, and none of them took any food. It was found that when ripe the males could be distinguished from females of the same size by three peculiarities: the proportionately greater size and prominence of the eyes, the bluntness of the snout, and the presence of pigment on the ventral surface.

All the large conger sent to market, which vary from 3 ft. to 6 ft. or 7 ft. in length, and which sometimes exceed a weight of 100 lb., are therefore females. It was proved by the Plymouth experiments that female conger in the Aquarium, although they feed voraciously and grow rapidly for some time, always sooner or later cease to feed, live for six months or so in a fasting condition, and then die, and that such specimens always contain enormously developed ovaries. There can be no reasonable doubt that in the natural state conger of both sexes cease to feed when the generative organs begin to mature, and that they die after spawning. They spawn therefore but once, and reproduction is followed by death. In specimens which have died in the aquarium in the gravid condition, it was found that all the organs except the ovaries were much reduced, and the skeleton in particular undergoes extraordinary retrogressive changes. The mineral matter disappears from the bones, so that they can be cut like cheese, and the teeth are all lost.

That the condition is not due to disease, or the result of captivity, is proved by the constancy with which it develops, and by the fact that the ovaries are healthy and rapidly develop. The ova, however, never became perfectly ripe, and have never been shed in the aquarium. In all probability the premature death of the females is due to the absence of natural conditions, especially of the pressure of the water at the depth at which the conger naturally spawns, a depth of at least thirty to forty

fathoms, and probably much more. The males, however, as stated above, continue to live in the aquarium for months after their reproductive organs are perfectly mature, and their ultimate death seems in no way hastened by the artificial conditions of their captivity.

The larva of the conger has been known to naturalists since 1763 under the name of *Leptocephalus morrisii*. It is a small transparent fish, much compressed from side to side, broad in a vertical direction, with a proportionally small head, from which last character the name *Leptocephalus*, meaning "small head," was suggested. The median fin is narrow, the pelvic fin absent, the pectorals small. A large number of specimens of this curious type were obtained from different parts of the world and described as distinct species, but in 1864 the American naturalist Gill came to the conclusion, for anatomical reasons, that the *Leptocephali* were the young stages of the eel family, and *Leptocephalus morrisii* in particular was the larva, of the conger. The truth of this conclusion was placed beyond a doubt by the French zoologist Yves Delage, who obtained a living specimen of the creature in question at Roscoff in Normandy, in February, 1868, and kept it alive till the following September. Between April and July the *Leptocephalus* underwent a gradual but complete metamorphosis into a young conger. The latter at the end of the transformation was  $3\frac{7}{10}$  in. long. The *Leptocephalus morrisii* is from 4 to  $5\frac{1}{2}$  in. or even 6 in. in length, and during the metamorphosis a distinct reduction in length takes place. The *Leptocephalus* is ribbon-shaped and transparent, and has no red blood-corpuscles nor air-bladder. The young conger has red blood-corpuscles, a round body, a pigmented skin, a head of normal proportions, and a well-developed air-bladder.

In 1888, among a large number of pelagic marine fish eggs from the Bay of Naples, the Italian naturalist Raffaele described five different kinds of which he could not discover the parentage, but which had a close resemblance to one another, and which in his opinion probably belonged to fishes of the eel family. This opinion was chiefly founded on the characters of the larvæ hatched from the eggs in question. These larvæ were of much elongated form with a large number of muscle segments. Shortly after hatching they developed in the lower jaw peculiar

long teeth which projected beyond the mouth, and there can be little or no doubt from the results of more recent investigations described below, that these larvæ were Leptocephali.

The Italian zoologist Grassi when he was professor at the University of Catania, carried out in collaboration with Calandruccio, a thorough investigation of the numerous Leptocephali of the Straits of Messina. By keeping specimens alive in aquaria, as Delage had done so successfully in the case of the larva of the conger, these Italian naturalists traced the development of a whole series of Leptocephaline forms into different species of the eel family, but the most interesting and most important of their identifications was that of the larva of the common eel. This discovery was made in 1893, and the species of *Leptocephalus* which was found to develop into the eel was one named *L. brevirostris*, described by Kaup in 1865 in a catalogue of the specimens in the British Museum. The distinguishing characters of this form are its rather small size, not exceeding 8 cm. or 3 in. in length, its short snout, the number of segments, not exceeding 118, the number of teeth, 14 in each jaw, and the distinct tail-fin. It is noteworthy that the specimens examined by Kaup came from the Straits of Messina.

Grassi and Calandruccio obtained specimens of Leptocephali in various ways, sometimes from fine-meshed nets used by fishermen in shallow water near shore, sometimes from the sea-shore where they found them stranded. In March, 1905, they saw several thousand specimens which had been thrown up by the waves near Faro. They also frequently obtained specimens from the stomach of the sun-fish (*Orthagoriscus mola*), which they regard as naturally an inhabitant of deep water. They concluded from their experience that the Leptocephali were naturally hatched and developed at great depths, and were brought to the surface or the shore by the strong currents and whirlpools for which the Straits of Messina are famous. This view was supported by the condition of the adult eels which they obtained from time to time which, although not actually mature, were certainly more advanced towards sexual maturity than ordinary eels taken in fresh water. Their genital organs were more developed, and in the males occasionally ripe spermatozoa were found. Petersen in Denmark in 1894 had pointed out that the eel when migrating to the sea and passing into the breeding

condition undergoes a change in external characters : its skin, previously yellow in colour, becomes silvery, its pectoral fin becomes black, and its eyes become larger. These differences, especially the large size of the eyes, were distinctly recognisable in the specimens obtained from the sea by Grassi. Eels in this condition were frequently found in the stomachs of sword-fish; the capture of which is a regular industry off the coast of Sicily. The great increase in the size of the eyes in eels in the sea is in all probability an adaptation to life at considerable depths, for it is well known that deep-sea fishes have large eyes except in a few cases in which eyes are absent altogether. The conclusion of the Italian investigators is that the eel spawns naturally at a depth of about 200 fathoms. The coast of Sicily, especially in the neighbourhood of Messina and the north-east corner of the island generally, is very steep, so that the depth of 200 fathoms is reached at a short distance from land.

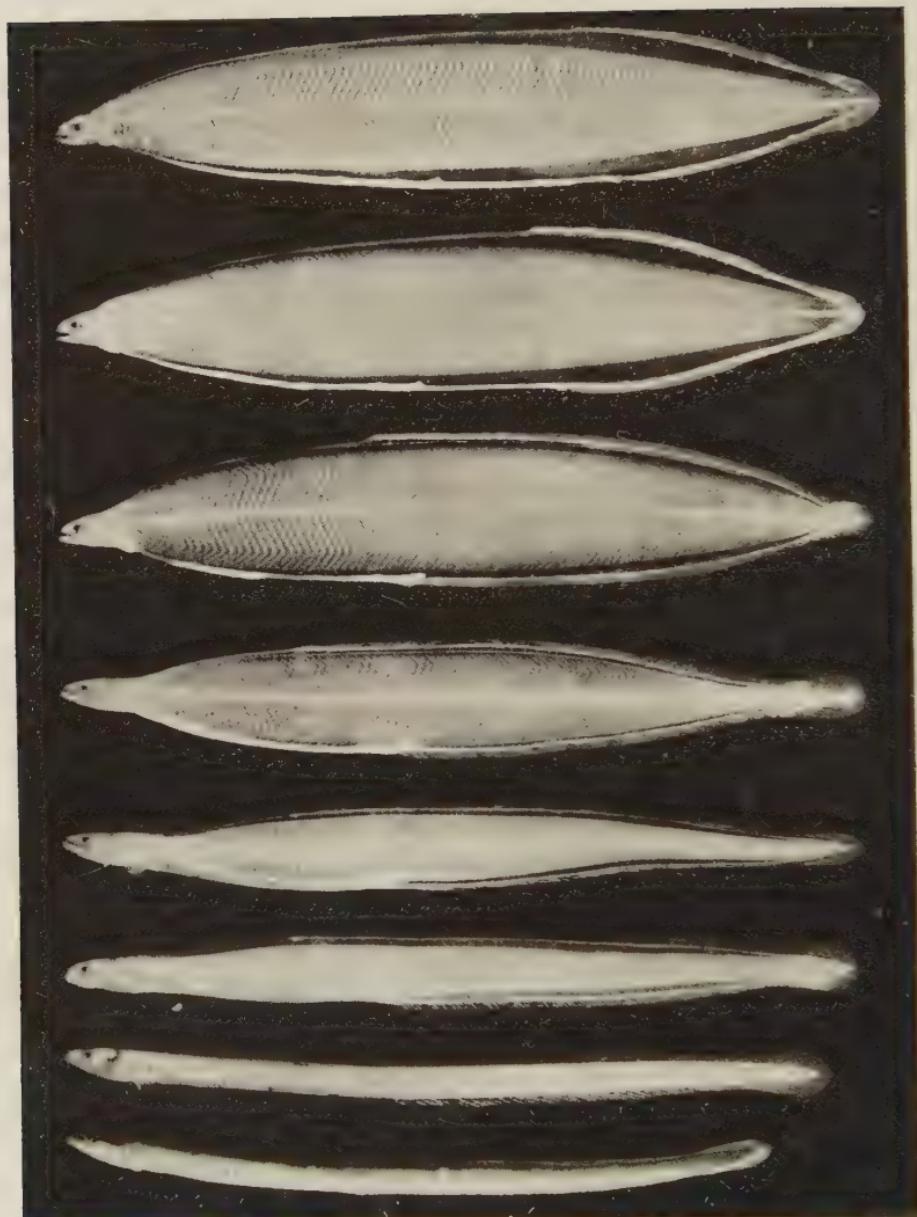
It seemed at first very improbable that the eels of the British Islands and of north-western Europe would have to migrate to a depth of 200 fathoms in the sea in order to spawn, for the 100 fathom line passes a long way west of the English channel, outside the west of Ireland and Scotland, to the north of the Shetlands, and only approaches the coast along the south of Norway. Consequently eels from the Thames or the Elbe would have to travel all the way to the west of Ireland or to the south coast of Norway before they reached the depths which were supposed to be necessary for their reproduction by the Sicilian naturalists. Evidence, however, has recently been obtained that this extraordinary migration actually takes place and that the elvers which ascend our rivers on the east coast as well as on the west, or which make their way to the waters of central Europe, were hatched in the great Atlantic far beyond the 100 fathom line. The most important part of this evidence is the result of the work of Johannes Schmidt, one of the Danish naturalists engaged in the International Fishery Investigations.

One important problem in connection with the history of the common eel north of the Mediterranean was to ascertain where the *Leptocephalus brevirostris* was to be found. One specimen of this form was identified by Günther among the collections of the "Challenger"; it was taken on the surface in the At-

lantic off the west coast of Africa. Schmidt, however, found that the identification was not correct. One specimen was taken by Schmidt himself in 1904 on the Danish research steamer *Thor*, to the west of the Faroes at the surface. Another was taken by Mr. Holt in August of the same year off the west of Ireland. In 1905 Schmidt took the investigation steamer *Thor* southwards from the Hebrides to the Bay of Biscay, following the course of the 500 fathom line, and fishing with large pelagic nets from time to time. As he went south he obtained increasing numbers of the larval eel until off the entrance of the English Channel at the end of June,  $49^{\circ} 25' N.$ ,  $12^{\circ} 20' W.$  he captured as many as seventy specimens in a two hours haul. Further south in the Bay of Biscay, specimens became scarcer and finally none were found. The chief spawning ground of the eel therefore lies to the west of the Channel at depths between 500 and 700 fathoms. The larvæ, however, do not live at or near the bottom. Some were taken at the very surface, but they were most abundant at a depth of 50 fathoms, approaching nearer to the surface at night. When placed in vessels of sea-water with sand and mud at the bottom, they showed no tendency to burrow, although they avoided the light. They swam with eel-like undulatory movements of the body. They were of glassy transparency, only the eyes having a silvery appearance. With them were captured enormous numbers of other pelagic creatures, most of them, like the eel larvæ, of glass-like transparency; of other fish-larvæ there were the *Leptocephalus* of the conger, the larvæ of *Fierasfer*, of the angler, of a species of ling, of several species of Gadidæ, and of some Pleuronectidæ; of invertebrates, the most abundant were pelagic Ascidiants, especially *Salpæ*, crustacea and molluscs. The occurrence of the *Leptocephalus* of the conger shows that this species also probably migrates to depths of some hundreds of fathoms in order to spawn, and this would make it still easier to understand why the females fail to spawn in aquaria.

On 31st August and 1st September a few other specimens of the eel larva were taken between St. Kilda and Rockall which were more advanced in their metamorphosis. In March and April the young eels which have almost completed their metamorphosis, though still perfectly transparent (glass-eels, Plate XXIX., 7), have been taken at the surface at night in the North





STAGES IN THE METAMORPHOSIS OF *LEPTOCEPHALUS BREVIROSTRIS*,  
THE LARVA OF THE COMMON EEL  
(AFTER JOHANNES SCHMIDT)

1. EARLY LEPTOCEPHALUS STAGE OCCURRING NEAR SURFACE IN ATLANTIC. 2—6. REDUCTION  
IN VERTICAL BREADTH AND FORWARD EXTENSION OF FINS. 7. GLASS-EEL FROM NORTH SEA.  
8. PIGMENTED ELVER

Sea, but in the day time they are only to be caught at or near the bottom. Between February and May these young eels, which are about two inches in length, reach the coast and begin to ascend the rivers. It has been proved that the ascent commences earlier at places nearer to the Atlantic, later at places more remote; thus in the Severn the ascent commences in February and takes place chiefly in March and April, in Denmark it does not begin till May. It will be seen therefore that the young fully developed eels which ascend rivers are already nearly a year old; the Leptocephali were taken in the Atlantic in June and must have been hatched before that, while the earliest ascent is in February following. These young eels therefore are the progeny, not of the adults which went down to the sea in the preceding autumn, but of those which descended the year before that.

The principal changes of the metamorphosis, stages of which are represented in Plate XXIX., are as follows. In the early *Leptocephalus* stage the body is very deep from the dorsal edge to the ventral and narrow from side to side, the anus is about one quarter of the total length from the end of the tail, and the dorsal and ventral fins begin at the level of the anus. The mouth is furnished with long larval teeth projecting forwards. These teeth soon disappear. The average length of this first stage is 7·5 centimetres or 3 in.; the average length of the fully developed and pigmented young eels is 6·5 centimetres or  $2\frac{3}{5}$  in., while some of them are only  $2\frac{1}{5}$  in. long. During the metamorphosis the anus and the commencements of the dorsal and ventral fins move gradually forwards, the dorsal fin more than the ventral; the head does not grow but the body is reduced to the thickness of the head. During the whole transformation the larvae seem to take no food, a fact which accounts for the reduction of size. With regard to the abundance of young elvers ascending rivers the following figures are given in an official report by Buckland and Walpole published in 1876: 1400 to 1500 elvers make 1 lb.; as 1 cwt. of elvers are frequently taken by one man in one night in the river Severn and hundreds of men are taking them at the same time, some idea may be obtained of the prodigious number that annually enter that river.

Our knowledge of the eggs of the eel and conger is much

less definite than that of the larvæ. In 1888, as already mentioned, Raffaele described five different kinds of eggs obtained at Naples, which, from the structure of the larvæ hatched from them, he considered to belong to species of the eel family. These eggs were large for pelagic eggs, and most of them possessed oil-globules; one kind however was without an oil-globule, and this one was considered by Grassi and Calandruccio to be that of the common eel; this opinion has not been confirmed, for the structure of the immature eggs in the roe of the conger and eel indicates that the eggs when shed are provided with an oil-globule. No eggs similar to those of Raffaele have been yet taken in the Atlantic on the European side, but in 1900 some pelagic ova were taken about thirty miles from the American coast in July which hatched into Leptocephali and were considered to belong probably to the conger; these eggs had a single large oil-globule. These eggs appear to have been taken at the surface, but as such captures are so rare it seems probable that, as Schmidt believes, the eggs of *Anguillidæ* are not only shed at the bottom at great depths, but usually remain there till hatched, suspended in the water; Schmidt has shown that the eggs of *Argentina* develop in this condition, and he calls such eggs bathypelagic. Two Leptocephali were also taken by the Americans off the coast of the United States and identified by Eigemann and Kennedy as belonging to the American fresh-water eel, which, however, is distinct from the European species and is called *Anguilla chrysippa*.

The ages to which eels attain before migrating to the sea in order to spawn have been investigated by Gemzoe at the Danish Biological Station. Petersen's statistical method by which numbers of specimens are separated into age-groups whose ages differ by one year, was found to be applicable only to the younger eels, because in consequence of variation in the rate of growth the annual groups in the larger specimens graduate into each other and can no longer be distinguished. The age of the mature eels was ascertained by counting the number of annual zones on the scales, the otoliths which exhibit such distinct lines of growth in plaice and other fishes being small and useless for age-determination in the eel. The scales of the eel are rudimentary and completely embedded in the skin, but like those of other fishes they exhibit on the outer side con-

centric rings of small calcareous plates. These plates vary in size and form successive zones, the outer rings of each zone being narrower and more closely crowded together while the inner are broader and therefore farther apart. The inner rings are formed in spring when the eel begins to feed after the period of hibernation, while the narrower rings correspond to the diminution in the rate of growth which takes place in autumn. Each zone therefore indicates one year of growth and the total number of zones shows the number of years which has gone to the growth of the scale. As however the scales are not developed until the eel is two years of age, this number has to be added to the number of annual zones in the scales to obtain the total age of the fish. In this way it was found that male silver eels, that is males which had assumed the breeding livery and were descending to the sea, were for the most part  $5\frac{1}{2}$  to  $6\frac{1}{2}$  years old, while the females were two years older or  $7\frac{1}{2}$  to  $8\frac{1}{2}$  years. In the eel, therefore, as in other fishes the males reach maturity at an earlier age than the females. A few males were found which were only  $4\frac{1}{2}$  years old and a few which were  $7\frac{1}{2}$ , but only in one case was the maximum of  $8\frac{1}{2}$  years indicated. Females more than  $8\frac{1}{2}$  were also rare, but the following record of older females is given with the corresponding lengths:—

86 cm. (34·4 in.)	.	.	.	.	.	.	.	$10\frac{1}{2}$ years.
87 cm. (34·8 in.)	.	.	.	.	.	.	.	$11\frac{1}{2}$ years.
96 cm. (38·4 in.)	.	.	.	.	.	.	.	$11\frac{1}{2}$ years.
96 cm. (38·4 in.)	.	.	.	.	.	.	.	$11\frac{1}{2}$ years.
96 cm. (38·4 in.)	.	.	.	.	.	.	.	$12\frac{1}{2}$ years.

Apparently in individual cases eels live to much greater ages than these without assuming the breeding livery or migrating to the sea. It is supposed that for some unknown reason such eels are sterile; it is certain that they show no signs of maturation of the reproductive organs. One specimen which died in an aquarium in 1877 was stated to have lived in captivity for twenty-two years, and another is mentioned by Day which lived for upwards of thirty-one years in a well and was then choked by a frog which it tried to swallow.

It is not certain how long a time elapses between the descent of the silver eels to the sea and the actual process of spawning. The descent takes place in autumn and the evidence

obtained from the recapture of marked specimens in the Baltic indicates that the journey from the Baltic to the spawning grounds in the deep Atlantic occupies about six or seven months, so that spawning probably takes place in the April or May following the migration.

*Diseases.*—Diseases are best known in fresh-water fishes and, as in man, are usually due to microscopic parasites. The salmon disease has already been mentioned. Parasitic protozoa cause a disease in flounders; the symptom is the presence of little white tubercles on the skin of the fins and body; these tubercles contain multitudes of microscopic spores. A similar disease has been observed in fishes of the carp family (*Cyprinidæ*) and may be epidemic. Larger parasites of various kinds both external and internal abound in fishes, both marine and fresh-water, but many of them are constantly present, and unless in exceptional numbers, can scarcely be said to produce disease. So many fishes end their lives by being devoured by other fishes and other animals, that cases of natural death, especially in the sea, are comparatively rare; a few cases such as that of the tile-fish and the salmon, the eel and the conger, have been mentioned, but of old age and natural death in the majority of species we know nothing.

## CHAPTER VII

### VARIATION

Continuous variations, their mathematical investigation, and relation to locality. Discontinuous variations or mutations, e.g. in flat-fishes. Variation under domestication.

**I**T is well known that no two individual animals are exactly alike, and the small differences which are always present between individuals are technically known as continuous variations, as when a large number of specimens are examined they can be arranged in a gradual series of steps below and above the degree of the character which is most frequent. On the other hand, there occur occasionally conspicuous abnormalities which are not known to be connected by intermediate stages with the typical form, and these are called discontinuous variations. Latterly the term mutations has been frequently applied to such variations.

Continuous, i.e. small individual variations, have been studied in some of the common British fishes of greatest commercial value with great minuteness, for example in the plaice.

In this species, as in most fishes, they are well exhibited by the number of the fin-rays; as in this species there is some difference between the sexes, it is necessary to treat the males and females separately.

The character and extent of such variations are most satisfactorily exhibited in the form of a curve or diagram, such as that shown in Fig. 29, which represents the numbers of dorsal rays observed in a sample of North Sea plaice; the total number of fish in the sample, all females, was 91. The figures at the base of the diagram are the numbers of rays, those at the left the numbers of fish in which the different numbers of rays occurred; thus, it is shown that the most frequent number was 72, which occurred in fifteen fish, while the numbers 67 and 79 occurred in only one specimen in each case. Other

characters whose variations have been studied in the plaice, are the number of the tubercles on the head, the number of gill-rakers on the first branchial arch, the breadth of the body and length of the head in proportion to the total length, and the degree of spinulation of the scales. The number of tubercles on the head in the great majority of specimens is five, occasion-

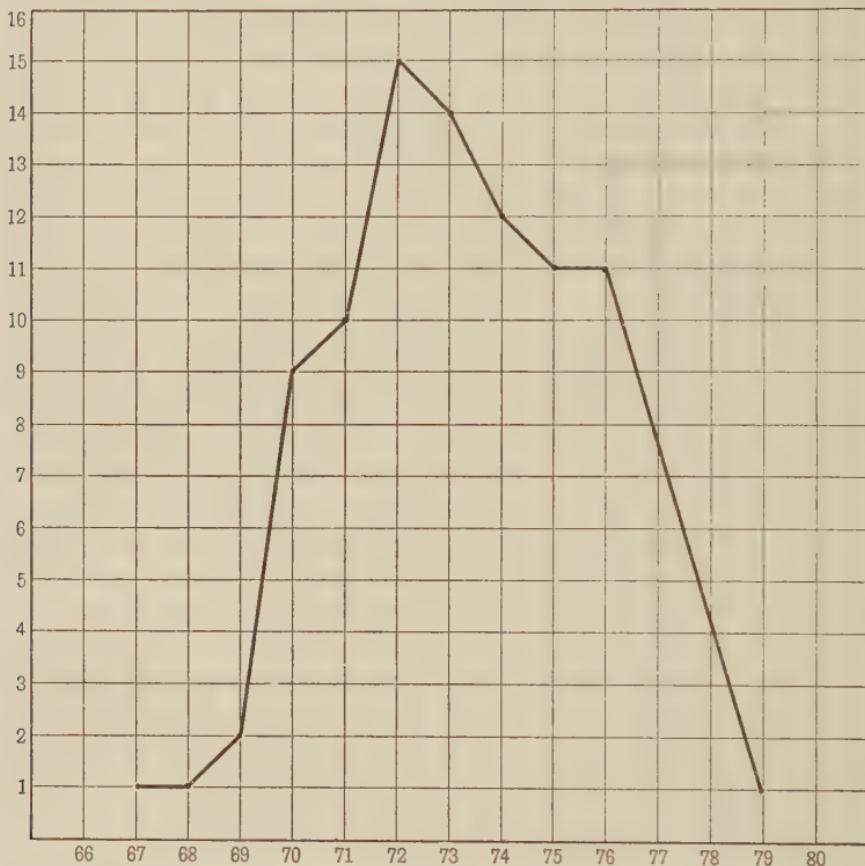


FIG. 29.—Variation in number of dorsal fin-rays in a sample of North-Sea plaice.

ally more or fewer occur. The presence of minute spines on the scales is a secondary sexual character usually confined to mature males: when least developed, it is present only on the fin-rays; in other cases it occurs also on the head, in others extends to the body as well. By thus studying the range of variation for several characters, it is possible to distinguish local forms or varieties when single individuals cannot be distinguished. Thus there are indications that the number of fin-rays is less and

the spinulation greater in plaice of the northern part of the North Sea, than in those of the southern part. The differences are more distinct when we compare plaice from the Baltic with those from the North Sea, the number of fin-rays being less, and the spinulation greater in the former than in the latter.

Such slight differences in the characters of samples from different localities are of very frequent occurrence in species both of animals and plants, and they give rise to problems which are by no means fully solved. They seem to be due to the difference of conditions in the localities, and there is some evidence that they are due to the direct influence on the individual and are not constant and hereditary. But it is difficult to see how the conditions should affect the characters in question, why for example the conditions of the Baltic should produce a reduction of fin-rays and greater spinulation. We cannot trace a general influence as in the case of the relation between light and pigmentation, nor have we any evidence that the differences are due to mechanical or functional stimulation, or to selection. With regard to the last factor it is impossible to believe that small variations in many of the specific characters we are considering could be selected by their direct utility to the individual, because the characters themselves, so far as we can see, have no utility. We have no evidence that the tubercles on the head, or the red spots, are of any benefit to the plaice, although they serve to distinguish that species from the flounder; the spinules may be due to some kind of mechanical stimulation involved in the habits of the males, but they can scarcely be of any use. On the other hand, the fins are important functional organs, and a difference in their extent involves a difference in the number of fin-rays. The scales of Teleostei afford some of the most important specific characters, and these characters exhibit continuous variations, but there is no sound reason for the belief that the scales are of any benefit to the fish at all. They are rudimentary in the plaice, represented in the flounder and the turbot only by scattered tubercles; the brill has regular spiny scales, and in these and a vast number of other cases it would, as far as we can see, make no difference to the survival of the fish if the scales or tubercles were altogether absent.

Mr. Garstang has investigated the variations of the mackerel,

which as a species is found on the coasts of both Europe and North America. The chief characters which he examined were the number of transverse black bars on the sides, the number of spots between the bars, the number of dorsal finlets, and the number of fin-rays in the two dorsal fins. In all these characters there was a range of variation, and although in samples from different regions the ranges overlapped, the investigator obtained evidence that the "mode" or most frequent variation in American fish was different from that in European samples, and further that there was a similar but smaller difference between Irish mackerel and those from the North Sea and English Channel. The American mackerel showed the highest averages in the following characters: (1) the number of transverse bars, (2) the number of spots, (3) the number of dorsal finlets; while they yielded the lowest averages in the rays of both dorsal fins. Mr. Garstang draws the conclusion that although the mackerel is considered a migratory fish, it does not migrate to so great an extent as formerly supposed; that it certainly does not cross the Atlantic. This is a necessary conclusion with regard to the adult fish, but it is still an open question whether the differences are hereditary or whether European mackerel, if reared in American waters, would develop the characters of the American fish. It also follows that the fish of the south and west of Ireland do not as a rule migrate into the English Channel or North Sea and vice versa.

Similar statistical studies of continuous variation have been made by Professor Eigenmann on *Leuciscus balteatus*, a species living in the Columbia and Frazer Rivers of western North America and belonging to the same genus as our own minnow, roach, chub, and dace. He found a great range of variation, especially in the number of rays in the ventral fin. In all the fresh-water fishes of the Pacific slope of North America there is a much greater range of variation than on the Atlantic slope, both in the characters of allied species and the individuals of a single species. In the case of *Leuciscus balteatus* Eigenmann found that every locality had a variety peculiar to itself, each different in the average number and in the curve of variation of the ventral rays. For example, in the Frazer River seventy-nine specimens were collected in water affected by the highest tides of the sea, fifty-nine at an elevation of 1300 feet in the upper

part of the course of the river, and fourteen specimens were taken still higher up at an elevation of 1900 feet; in the first sample the most frequent number of ventral rays was 19, in the second it was 17, in the third it was 15. Thus the number of rays decreased with the altitude and at the same time the range of variation was also decreased. Similar results have been obtained in other species, and are attributed to the great differences in climatic and geological conditions, not only in different streams, but in different parts of the same stream, on the Pacific slope. Of course such local differences could only exist in a non-migratory species such as the *Leuciscus* in question, but as was pointed out above we do not know how far the differences are permanent and inherited, and whether they would disappear in fishes which developed and grew in the same locality although produced by different local varieties. Professor Eigenmann discusses the question of the kind of influence exerted by the environment, asking whether it is merely selective or directive: "Is the variation promiscuous and inherent in the species, or is it determinate and forced in certain directions by the environment? The latter seems to me the better way of reading such variations as are represented by the many curves which show a greater variation towards an increased number of rays than towards a decrease of rays. Here the variation is not promiscuous but definitely determinate." It is possible in this case that the variation is connected with the increase or decrease in the functional use of the fin, but in other cases no direct influence on the varying organ can be traced.

Another remarkable case in which a relation of variation to local conditions is evident is that of the trout. A complete series of transitional forms has been traced between the common brook-trout and the anadromous sea-trout. They vary in form and colour, in the number of cæcal appendages of the intestine and in the vomerine teeth, while the differences in adult size are enormous. There are land-locked lake-trout like that of Loch Leven, small brook-trout like those of Cornwall, never more than a few inches in length, and estuarine trout which are scarcely distinguishable from true sea-trout, which in its turn is different on almost every part of the coast. Numbers of species of trout have been named by various systematic

ichthyologists, but their permanence is now rejected by the best authorities. Trout and salmon have both been introduced into Tasmania and New Zealand. The former have become established and in many cases have become very much larger fish, differing considerably from their European ancestors, while the true salmon having descended to the sea as they reached the smolt stage, have always failed to return. The salmon, *Salmo salar*, is a true species, distinguished from the various forms of trout by having less than thirteen scales in a transverse series from the posterior border of the adipose fin to the lateral line. The various varieties of char, on the other hand, of which almost every lake in Great Britain and Ireland has one, are not species but varieties of *Salmo alpinus*, which is migratory and occurs in the north of Europe; the "ombre chevalier" of the Swiss lakes, and the saebling of the lakes of Austria and the Bavarian Alps are also varieties of the same species.

Discontinuous variations or mutations are best known among the Pleuronectidae or flat-fishes. One of these mutations is of a kind which occurs also in other asymmetrical animals, and consists in a complete reversal of the usual asymmetry. It has already been mentioned that some species of flat-fishes are normally right-sided and others left-sided, but it frequently happens that a left-sided specimen of a species normally right-sided is found, or vice versa. In the flounder, which is normally right-sided, reversed specimens are very common. In these specimens the eyes and colour are on the left side instead of the right, but there is nothing else abnormal about them. At Plymouth left-sided flounders are almost as numerous as right-sided, and the fishermen sometimes state that one kind are males and the other females, but there is no truth in this. It is a curious and important fact that the position of the internal organs is not affected by the asymmetry of the fish, whether in species which are normally left-sided like the turbot or brill, or abnormally so as in reversed specimens of the flounder. In fact, in all flat-fishes the liver is on the left side and the coils of the intestine on the right, and the adaptations of the eyes, the mouth, the fins, and the colour have left the internal organs unaffected. Among the other asymmetrical animals in which reversed individuals occur may be mentioned the spiral-shelled molluscs called Gastropods: in these the spiral shell is usually

a right-handed spiral, but some species are left-handed, and in right-handed species left-handed specimens occasionally occur.

Abnormalities of coloration are also frequent in flat-fishes. In some cases pigment is present on the lower side as well as on the upper in varying degrees from a few small spots to complete pigmentation of the lower side. In these cases the presence of the pigment must be considered to be independent of any influence of light, and at first it seems difficult to reconcile the occurrence of such variations with the conclusions drawn from the experiments described in a subsequent chapter on the influence of light. Consideration of the facts, however, shows that the same effect, pigmentation of the lower side, may be due in different cases to two quite different causes, namely the action of light and spontaneous variation, just as a man may be born blind or may become blind from disease or injury. When the lower side is exposed to light the pigment develops gradually, whereas in those specimens which are found with lower sides pigmented in nature we have no reason to suppose that the lower sides have been exposed to light, or that the pigment developed gradually. The congenital nature of the abnormality is still more evident in cases of the opposite condition, when areas of greater or less extent on the upper side are white. When as sometimes happens the whole or nearly the whole of the lower side is coloured like the upper the specimen is said to be ambicolorate, and this condition is associated with a structural similarity of the two sides. In the turbot and flounder there are no regular scales in the skin, but in their place there are spiny, calcified tubercles scattered all over the upper surface in the turbot, confined to the bases of the fins and the region of the lateral line in the flounder. In other cases, as in the sole and dab, the scales are spinulate, or bordered with minute spines. In all such cases the dermal structures are, in normal specimens, less strongly developed on the lower side than on the upper, but in ambicolorate specimens the armature is equally developed on both sides; the specimen is "ambiarmate" as well as ambicolorate. Even when there is only a well-defined patch of colour on the lower side the armature within this area usually resembles that of the upper side, while in the white part it is less developed. This increased development of the armature could not be due to the influence of light.

A very remarkable structural peculiarity occurs usually in specimens which are completely ambicolorate, or nearly so. This has been observed most frequently in the turbot and flounder, especially in the former, but is not unknown in other species. It consists in the condition of the anterior end of the dorsal fin, the attachment of which stops short behind the upper eye, while the fin itself projects forwards as a hook-shaped process as seen in Plate XXX., Figs. A and B; the upper eye itself also seems to lie on the edge of the head and to be directed more outwards than in normal specimens. A specimen of the turbot in this condition was formerly described as a distinct species under the name *Pleuronectes cyclops*, and the malformation is sometimes described as cyclopean, but there is no union of the two eyes to justify the use of this term. In the turbot and flounder, as well as in the brill and plaice, this malformation of the head is always present in completely ambicolorate specimens, and in the turbot when only the head region of the lower side is white the malformation also occurs, but when the coloration of the lower side is of less extent the malformation is wanting and the head is normal. On the other hand, ambicolorate specimens of the sole and lemon sole (*Pleuronectes microcephalus*) have been observed in which no malformation of the head occurred.

Cases of the opposite kind of abnormal coloration in which more or less of the upper side is white like the lower are not uncommon in the plaice and in other species, and usually the white area of the upper side is sharply separated from the adjacent coloured surface. I have seen a sole twelve inches long in which the whole of the upper side was white like the lower, except the head and part of the tail-fin.

The most remarkable abnormality known in flat-fishes is that of a small turbot not quite two inches long which was captured in 1906 on the coast of Cornwall; in this fish (Plate XXX., A, B) the right side was white as usual, and the left side was normally coloured except on the head; but both eyes were on the right uncoloured side instead of the left; the malformation of the head above described was also present, the anterior end of the dorsal fin projecting forwards in a free, hook-shaped process. This specimen when alive rested on the ground with its white side and the eyes directed upwards, and



UPPER, RIGHT, SIDE OF ABNORMAL TURBOT 4·4 CM.  
LONG CAPTURED ON THE COAST OF CORNWALL IN 1906



LOWER, LEFT, SIDE OF SAME



LOWER SIDE OF NORMAL FLOUNDER AFTER EXPOSURE  
TO LIGHT FOR 14 MONTHS. ACTUAL LENGTH OF  
SPECIMEN 8½ INCHES



the coloured left side downwards. There was some colour on the upper or right side of the head, so that the condition of the fish would be nearly described by saying that the body was normal, but the head reversed.

Assuming that these abnormalities are mutations, and not due to any exceptional conditions of life or development, we must regard them as the result of abnormalities in the constitution of the eggs from which the fishes develop. According to a well-known theory of heredity, the egg is supposed to contain elements called determinants, corresponding with the parts of the body into which the egg develops. Thus, in the egg of a flat-fish we may suppose that there is a set of determinants for the right side and another set for the left; if these two sets have in a given egg changed places, that egg develops into a reversed specimen. In the abnormal turbot last described we may suppose that reversal has taken place in the head only, and so a reversed head is joined to a normal body, and this may be the reason why the anterior extension of the dorsal fin is not attached to the head, the two parts not being in proper relation to each other. This leads to the idea that a similar explanation accounts for the malformation of the head in ambicolorate specimens: we may suppose that in these the head is normal, and the body reversed, so that the upper side would be originally white, but has become coloured from exposure to the light. As an alternative hypothesis we might suppose that in ambicolorate specimens, two coloured sides were united in the same egg, instead of a left and right as in normal cases. It is unnecessary to discuss these hypothetical explanations more in detail: enough has been said to indicate how such congenital abnormalities may arise from peculiarities in the egg, and to show that their occurrence is not necessarily inconsistent with the view that the normal characters of flat-fishes were originally caused by the habit of lying on one side, and the changes in the use of organs, and in the influence of light which resulted from this habit. If it were true that the peculiarities of flat-fishes were due to the "inheritance of acquired characters," the fact would still remain that the peculiarities are hereditary and therefore liable to mutations like any other hereditary characters. Moreover, the nature of these remarkable abnormalities affords no evidence of the possible occurrence of such spon-

taneous variations, as would be required to bring about the evolution of flat-fishes on the view that acquired characters cannot be inherited; the mutations are all in the direction of greater symmetry, or a mere reversal of asymmetry, whereas in the evolution of a flat-fish from symmetrical ancestors, mutations in the direction of asymmetry would be required, and it has never yet been shown that mutations which could lead to the condition of flat-fishes occur in ordinary symmetrical fishes, which swim in a vertical position. A still stronger argument may be founded on the gradual development of the peculiarities of the flat-fish, the process of metamorphosis. The mutations to which we have referred in these fishes, and many other congenital variations in other animals, develop directly, not by a gradual change from a preceding condition.

We have every reason to believe that the abnormalities above described are present from the beginning of the metamorphosis. There is no reason to suppose that the flat-fish was first normal and gradually became abnormal. On the other hand, the mutations which would be required to produce the evolution of the normal Flat-fish from a symmetrical ancestor would consist in gradual changes such as we now see in the metamorphosis. We are not, therefore, justified in assuming, as most evolutionists at the present day would assume, that the abnormalities in question are examples of the same kind of variation as that which gave rise to the Flat-fish originally. On the contrary, it is more reasonable to regard the two things as quite distinct and different: the abnormalities as due to mutations arising in the ovum, the original evolution of the flat-fish as due to modification caused by the peculiar habits.

Various well-known variations have arisen in certain species of fish which have been domesticated for long periods. The origin of these variations has not been scientifically studied by modern methods but it seems most probable that they arose as mutations. The most familiar of them is the colour of the gold-fish, which is a domesticated variety of *Carassius auratus*, a native of China; it is doubtful if this species itself is really more than a variety of *Carassius vulgaris*, which occurs naturally in Europe and Siberia. The colour of the wild *Carassius auratus* is greenish or olivaceous, and that of the gold-fish is due to the reduction or absence of the black pigment which leaves the

coloured pigment everywhere visible ; this variation is called xanthochroism. When the coloured pigment is also wanting the fish is silvery. Besides the uniformly coloured varieties many others occur among gold-fishes, as may be seen in any pond where numbers of these fish are kept : some are black and silver, some black and red. These conditions are closely similar to the various uniformly coloured and pied variations seen in domesticated mice, rabbits, etc. ; in both cases the absence of all pigment, or albinism, occurs, either in part or all of the skin. The variety of gold-fish known as the telescope fish is distinguished by extraordinary monstrosities of the eyes and caudal fin ; the former are situated on outgrowths of the head like stalks, reminding one of the eyes in crabs and other stalk-eyed Crustacea, while the fin is doubled or split ventrally and the two halves are spread out horizontally or in the form of an inverted V. The telescope fish is reared principally in Japan and probably breeds true, but doubling of the tail-fin, absence of the dorsal and other abnormalities, occur frequently among specimens bred in Europe. Sir R. Heron in 1841 stated that the abnormal fish did not produce a greater proportion of abnormal offspring than the normal fish, but it seems probable that the inheritance of these mutations would be found to be Mendelian. Gold-fish were kept in China at a very early period and were introduced into Europe in the seventeenth or eighteenth century.

The common carp, *Cyprinus carpio*, which is distinguished by the possession of four barbels on the upper lip, is also a native of China and other parts of Asia. It has been kept in a domesticated state in China from ancient times and was introduced into Germany and France in the thirteenth century. In Germany, where until recently the supply of marine edible fish was limited to the coast, the cultivation of the carp has been continued to the present time ; in England, in the middle ages, it was kept in ponds by the monks as a supply of fish for Lent and Fridays, but its cultivation in this country has long been abandoned. In Germany among cultivated carp several distinct varieties have arisen. One of these is called the mirror-carp, and is distinguished by the greater size and lustre of the scales ; it has a small head and a thick body and grows to a large size ; some varieties of the mirror-carp have the scales

restricted to a single row along the lateral line, or to the back. Another variety, called the leather-carp, has no scales at all but owes its name to the much-thickened skin. Abnormalities of the fins also occur as in the gold-fish.

Gold-coloured varieties have arisen under domestication in two other species of Cyprinidæ besides the gold-fish. One of these is the ide, a species of the same genus as our dace and roach ; its scientific name is *Leuciscus idus*, and it is found in central and northern Europe. The golden variety known as the golden ide or orfe is bred in Germany. Two hundred specimens were introduced into the Duke of Bedford's ponds at Woburn Abbey in 1874 and lived there for many years. Similarly golden, red, and black-spotted varieties of the tench, *Tinca vulgaris*, have been produced under domestication in Germany, and occasionally introduced into England ; these colour variations are said by Siebold (1863) to occur in the wild state in Upper Silesia.

## CHAPTER VIII

### ADAPTATIONS

Shape, symmetry, colour. Flat-fishes, *Synodontis*. Locomotion. Flying-fishes. Respiration, gills and accessory organs. Air-bladder, respiratory and hydrostatic function. Sense-organs and senses. Hearing, relation of auditory organ to air-bladder. Sense-organs of lateral line. Sight. Divided eyes of *Anableps*, blind fishes.

**T**HE most striking instance of adaptation in shape and symmetry is that of the flat-fishes or *Pleuronectidae*.

These fishes habitually lie on the ground upon one side of the body, some species on the left side some on the right. In adaptation to this abnormal position the symmetry of the two sides is in many respects altered. If a flat-fish is held in a vertical position and compared with any ordinary fish many of the paired organs will be seen to be present in their usual position: on each side there is a lateral line, a pectoral and pelvic fin, and a gill-cover or operculum. The position of the gills shows which is the ventral edge of the body, and it is seen that the marginal fins are continuous dorsal and ventral fins, which in many species, *e.g.* the plaice or turbot, are distinct from the tail-fin, but in some species they are continuous with the latter. The direction of the mouth also is as in other fishes transverse to the median plane of symmetry, so that half of the jaws is on one side, half on the other. In plaice and sole, however, the two sides of the mouth are unequally developed, the jaws and teeth being much more strongly developed on the left or lower side where they are most used for seizing food. The most remarkable departure from symmetry is in the eyes, both of which are on the side which is naturally uppermost, that is to say the right side in a plaice or sole, the left side in a turbot or brill. The eye which is nearest the dorsal edge is that which belongs to the lower side, although it is separated from the latter by the dorsal fin: the other eye, the

ventral, which is nearer to the mouth, belongs naturally to the upper side. The asymmetrical feature next in importance is the difference between the two sides in colour: the lower side is white, the upper side coloured, the colours are dark brown ranging to black, with spots or markings ranging from yellow through orange to red; the plaice, for instance, is characterised by conspicuous red spots.

There are then three chief peculiarities in which a flat-fish resting on the ground with its original plane of symmetry in a horizontal position, differs from an ordinary fish which swims with its plane of symmetry vertical: (1) the position of both eyes on the upper side; (2) the absence of pigment from the lower side; (3) the extension of the dorsal fin along the line outside the dorsal eye, instead of between the eyes as in other fishes. In addition to these there are minor differences between the upper and lower sides: the scales or tubercles are less developed on the lower side, the pectoral fin on the lower side is usually smaller, and as already mentioned the jaws and teeth are usually larger on the lower side, reduced on the upper. Obviously these peculiarities of structure are all adaptations to the peculiarity of position and mode of life, and they serve as excellent examples of what we mean by adaptation. The flat-fishes are evidently descended from ordinary symmetrical ancestors which swam in a vertical position, and in the course of evolution their structure has undergone the modifications which are more suitable for their peculiar position and habits. To have a flattened shape and to lie upon the sand or gravel at the sea-bottom, is a mode of life which offers distinct advantages to a fish in the way of food or concealment from enemies, and it has been adopted by other fishes as well as flat-fishes. Skates, for instance, and the angler have adopted this mode of life, but they have always rested on the ground in the vertical position, and either were originally or have become flattened dorso-ventrally without alteration of their original symmetry. The ancestral flat-fishes must have been originally flattened from side to side, and therefore to obtain the advantage of contact with the ground were compelled to lie on one side. In this position the lower eye would be useless and therefore the head has been modified so as to bring that eye round to the upper side. Anatomy shows that the change is produced by a twisting or

torsion of the skull in the region of the eyes through an angle of  $90^{\circ}$ , and this twisting has taken place without affecting the symmetry of the posterior region of the skull, or the jaws and anterior region. The interorbital septum of the skull has been bent round from the middle line to the right side, in the sole for example, and the eyes lie on either side of the septum as usual. The bones which were originally below and external to the left eye have become larger, and a new connection on this side has been formed between the bones of the anterior and posterior region of the skull. Along this bony ridge which is now in line with the original dorsal edge of the body, the dorsal fin has extended, thus dividing the originally left eye from the left side of the face. The jaw-bones, instead of being twisted in the same manner, have actually become much larger on the lower side, so that the asymmetry of the mouth is in the opposite direction to that of the eyes.

The use of the tail as chief organ of locomotion is not suitable for a fish gliding along the ground, and we find both in skates and flat-fishes that the fish moves by undulations of lateral fins at the margins of the flattened body. The tail or caudal fin in both cases has become reduced, and the lateral fins much increased in extent. In the skates it is the pectoral fins which are lateral and are thus increased, in the flat-fish lying on its side the marginal fins are the dorsal and ventral, which have become increased so much that they extend from the base of the tail nearly to the anterior extremity. The dorsal fin in the sole extends to the anterior extremity of the head, in the turbot nearly as far, and even in the plaice and its allies as far as the middle of the dorsal eye. The ventral fin cannot extend so far forward, as it cannot pass in front of the anus, but the latter opening itself is shifted forward as far as possible so as to be near the gill-openings, and the pelvic fins occupy more or less of the small extent of margin left between the anus and the gill-apparatus. The dorsal and ventral regions of the flat-fish are thus much more similar than in other fishes, and in fact a new though imperfect symmetry is produced about the middle line of the upper side, which has to some extent replaced the original symmetry between the two sides; the bilateral symmetry characteristic of a vertical fish has given place to a dorso-ventral symmetry in the horizontal fish.

In these two features we find obvious functional advantages in relation to the conditions of life, and they are thus in harmony with the explanation of adaptations by the theory of natural selection, or survival of the best adapted. But in the third feature no such advantage is proved. The colour on the upper side is doubtless some advantage to the fish in masking it from enemies or from prey, and the benefit is much increased by the faculty which the fish possesses of changing the intensity of the colour to bring it into harmony with that of the ground on which it rests. The absence of pigment on the lower side, on the other hand, has never been proved to be of any benefit to the fish. The suggestion that this colour harmonises with the light coming from above when the animal is seen from a lower level, and is therefore useful in concealing the fish, is open to two objections. Firstly, the fish is not attacked from below, and always seeks protection by covering itself with sand, and secondly, when the fish is observed from below it appears as an opaque object shutting off the light, and is therefore conspicuous. There is very strong evidence that the reason why the lower side has lost its pigment is that it is shaded from the light. We do not know exactly how the action of light produces pigment, but in fishes at least we have good reason to believe that this action is necessary for the production of pigment in the skin. Fishes, like the cave-fishes *Amblyopsis* and *Lucifuga*, which live in the dark, are colourless, and fishes generally are colourless on the ventral side. The present writer, moreover, has shown that if flounders are kept alive in an apparatus which exposes their lower sides to light, pigment is gradually developed on the skin of the lower sides. The experiments were carried out at the Laboratory of the Marine Biological Association at Plymouth during the years 1890-1893. The apparatus consisted of a shallow tank the bottom of which was made of plate glass, on to which light was directed upwards by means of an inclined mirror. Young flounders soon after their metamorphosis were placed in this tank, and after a period varying considerably in different specimens, pigment precisely similar to that of the upper side began to show itself on the lower side. In some specimens kept under these conditions from one to three years the lower sides became almost as completely pigmented as the upper. Fig. C. on Plate XXX. represents one of these speci-

mens of which the lower side had been exposed to light for fourteen months.

In this case then the utility principle, in other words the idea of the theory of natural selection, is not applicable, and the question arises whether we are to call such a feature an adaptation or not. If we define an adaptation as a peculiarity of structure which is advantageous to the animal the word is not applicable to the absence of colour from the lower side of flat-fishes. But as the latter feature is due to the conditions of life, the others may have been produced in a similar way. The distortion of the eyes may have been caused in evolution by the constant efforts of the fish to direct the lower eye towards the light, that is to the upper side, together with the greater use of the muscles and bones on the lower side in connection with the jaws, but the latter condition does not seem to be necessary, for in many species, e.g. turbot and halibut, the jaws appear to be equally developed on the two sides. The extension of the dorsal and ventral fins may have been due to the greater use made of them. If this were true these two features would be due to the conditions of life acting not directly, as light acts on the skin, but indirectly by stimulating the functional exercise of the parts affected. It seems certain that all three peculiarities are in some way due to the conditions of life, and if we confine the term adaptation to these structural adjustments which have a definite function, a purpose, as it were, we require another term to indicate changes due to the conditions of life whether advantageous, indifferent, or even harmful. The best term for such changes is modifications, and we may define modifications as changes of structure produced in evolution from a more primitive condition, by changes in the conditions of life.

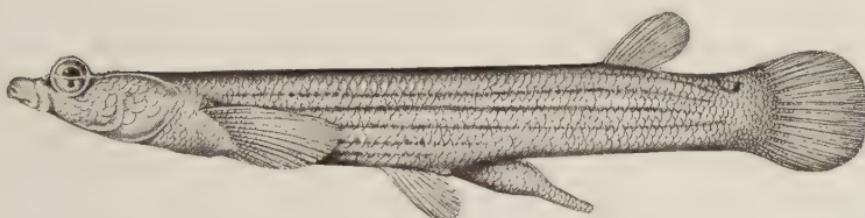
The close relation between the distribution of pigment on the skin of a fish and the incidence of light is remarkably shown by the peculiar pigmentation and the peculiar habits of various species of *Synodontis* (Plate XXXI., A), a genus of African Catfishes (Siluridæ). Many species of *Synodontis* which live in the Nile and other African rivers, but especially *S. membranaceus* and *S. batensoda*, are in the habit of swimming at the surface of the water in an inverted position, with the belly upwards. These same species have the pigmentation also

reversed, the ventral surface is dark brown the dorsal a light silvery grey. The peculiar habit attracted the notice of the ancient Egyptians who have represented the fish frequently in this unusual position. By the expression "distribution of pigment" used above is meant the presence of pigment on one part and its absence on another; the cause of the particular colours and markings such as spots and stripes in various patterns which are so conspicuous in some fishes is another question which is much more difficult to answer. The reason for the inverted position assumed by *Synodontis* seems to be unknown, but it may at least be said that the diminution of pigment on the dorsal side, which becomes the lower in the inverted position, is not known to be of any benefit to the fish.

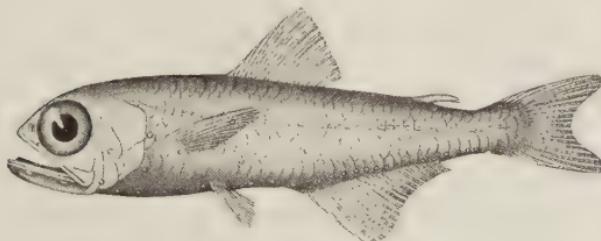
The most remarkable adaptation for locomotion among fishes is that of the pectoral, and to some extent the pelvic fins also, in the flying-fishes. In *Exocoetus* and its allies the pectorals are enormously enlarged, and lengthened, extending back to within a short distance of the tail. In *Dactylopteridæ*, the flying gurnards, the pectorals are even longer in proportion to the body. In the former the fins are used as parachutes, not being vibrated during the flight, but in the latter they are stated by observers to be moved rapidly up and down like the wings of a butterfly. Recently a fresh-water flying-fish belonging to a totally distinct family has been discovered in the Congo region, namely *Pantodon buchholzii*, belonging to the soft-finned sub-order Malacopterygii. The pectorals in this case are not so much elongated, but they are united to the body by membrane, and the pelvic fin-rays are separate and elongated as filaments; this little fish is only three and a half inches long, and was taken in its flight over the water by a butterfly net. Among the Gobies, the mud-skippers of tropical shores are adapted for hopping about the surface of the mud, using their pectorals, of which the bases are very muscular, as short legs. The head is raised on the pectorals in an attitude resembling that of the frog, and the eyes project upwards from the head, and are capable of free movement, whence the names *Periophthalmus* and *Boleophthalmus* given to the genera. They not only hop actively on the mud but climb on to mangrove roots, and move so quickly that it is difficult to catch them. They are unable to live under water more than a limited time, and in their



*SYNODONTIS BATENSODA*, A FISH OF THE NILE WHICH HABITUALLY SWIMS IN AN INVERTED POSITION



THE FOUR-EYED FISH, *ANABLEPS TETROPHTHALMUS*



*MYCTOPHUM REMIGER*, AN OCEANIC FISH WITH LUMINOUS ORGANS  
(AFTER GOODE AND BEAN)



*IPNOTOPS AGASSIZII*. (AFTER GARMAN)



habitual mode of life the tail-fin, which is richly furnished with blood-vessels, serves as an accessory organ of respiration. *Periophthalmus australis* is common on the shores of Queensland and grows to a length of twelve inches. In the various families of anglers, forming the sub-order Pediculati, the pectorals are modified for use as limbs rather than as fins, none of these fishes swimming freely in the water. The bones at the base of the fin are reduced to two or three in number and greatly lengthened, so as to resemble the bones of the fore-limb (radius and ulna) of a terrestrial vertebrate, and they form a kind of wrist joint with the broad part of the fin. In the angler and other forms which live on the bottom, they are used for shuffling along the ground. The pelvic fins are similarly modified, and indeed these are really more to be compared to fore-limbs, for they are situated in front of the pectorals and nearer to the middle of the ventral surface. The resemblance in attitude and locomotion to a frog or toad is greatest in the Malthidæ, e.g. *Malthe vespertilio*, in the West Indies.

The family of pipe-fishes, placed in classification in the same sub-order as the familiar sticklebacks, offers some striking examples of adaptation for concealment, or as it is technically termed protective resemblance. These fishes all live among sea-weed, and their slender stiff bodies, usually protected by bony scutes in the skin instead of scales, have more or less resemblance in colour and shape to fronds of the weeds. Thus one of the British species is bright green and in shape as well as colour is very similar to the blades of the sea-grass among which it is always found. The well-known sea-horse, *Hippocampus*, like the pipe-fishes, swims vertically and has a prehensile tail which he curls round stems of sea-weed. In an Australian sea-horse, *Phyllopteryx eques*, the resemblance is carried to a remarkable degree by the presence of branched flat appendages of the skin which have the same appearance as the fronds of sea-weed. Another extraordinary fish of this group is *Amphisile*, which lives on the coasts of the Indian and Pacific Oceans. This fish is almost as narrow from side to side as a knife-blade: the plates of the skin are united with the internal skeleton as in a tortoise: the small tail-fin is bent round to the ventral side, and the dorsal fins are at the end of the body. The fish swims vertically with its head

uppermost and cleaves the water with its razor-like ventral edge.

We have next to consider respiratory adaptations. The simplest and probably the most primitive condition of the branchial organs, at least in the true Pisces, is that which is presented by the Elasmobranchs. Here there is a series of wide transverse gill-slits at the sides of the pharynx, opening on the surface of the body and separated from one another by complete septa. The internal border of the septum is supported by a cartilaginous bar or "arch" from which radial rods of cartilage extend towards the outer edge of the septum. The actual respiratory organs are folds of the mucous membrane forming narrow leaf-like "lamellæ" on the anterior and posterior surfaces of the septa; these lamellæ are situated almost parallel to one another, radiating from the internal border of the septum towards the outer border, and projecting into short processes at their outer ends.

In other sub-classes the branchial organs exhibit a change in the relations of the branchial septa and branchial lamellæ, the former becoming reduced in different degrees and the latter becoming more independent and elongated, until in the typical bony fishes they are converted into long flat filaments attached to a narrow branchial arch by their bases only. The reduction of the septum is associated with the development of the gill-cover, which consists of a fold of skin growing backwards from the hyoid arch, *i.e.* the anterior boundary of the first cleft and supported by flat scale-bones. This operculum occurs in the Holocephali or Chimæroids, in which the gill-septum is so far reduced that it does not extend beyond the branchial lamellæ: but the latter are still attached along nearly their whole length. In the sturgeon, the septum extends little more than half the length of the folds, which project freely for the rest of their length, while in Teleostei as has been said, the reduction of the septum reaches its extreme and it forms merely an axis with a double series of gill-filaments extending outwards from it. In the lung-fishes (*Ceratodus*) the interbranchial septum is well developed, and the gill-lamellæ are attached to it along nearly their whole length.

The functions of the air-bladder are considered in another place: here we have to discuss certain peculiar adaptations

which enable fishes to breathe air. In some cases air is swallowed into the intestine, and the oxygen is absorbed by the blood-vessels of the mucous membrane. This is the case in one of the loaches, *Misgurnus fossilis*, which lives in stagnant waters in eastern and southern Germany, and in northern Asia. Intestinal respiration also occurs in species of South American Cat-fishes (Siluridæ and Loricariidæ), e.g. *Callichthys*, *Doras*, *Loricaria*, and *Plecostomus*.

In several other cases the adaptation for breathing air consists in a special modification of the gill-chamber enclosed by the operculum, an increase of surface being produced by complicated foldings of the walls, usually supported by bony plates. The organ so produced is known as a labyrinthiform organ. These organs occur in tropical fishes. Under tropical conditions both temperature and decomposition are unfavourable to the supply of dissolved oxygen in water, and these fishes have the power and the habit of living for considerable periods of time out of water and carrying on aerial respiration. One of the best known of such cases is that of the climbing perch, *Anabas scandens*. In *Anabas* and other allied fishes the organ consists of three or more concentrically arranged bony plates with frilled margins, attached to a bony base which in turn is attached to the upper end of the fourth gill-arch, and enclosed in a dorsal enlargement of the gill-cavity. The vascular membrane which covers the organ is supplied with venous blood by a branch of the fourth afferent branchial artery, and the efferent vessel from the organ joins the dorsal aorta. The possession of this organ enables the fish to breathe air for a long time, and although its climbing powers may have been exaggerated, there is no doubt that it has been observed frequently among vegetation on land. Its occurrence on the trunks of trees (palms and such tropical forms), seems on the whole rare and accidental. Daldorf stated in 1791 that he saw one of these fish on the stem of a Palingra palm near a lake in India. It was five feet from the ground when first observed, suspending itself on the projections of the bark by its gill-covers which are very spiny, and pushing itself upwards with its ventral spines. This fish, as well as the serpent-heads, also buries itself in the mud of ponds, or tanks, as they are called in India, when they are dried up in the hot season.

The other members of the family Anabantidæ are also fresh-water fishes, some occurring in estuaries but none in the sea. They are found in India, Burma and the Malay Peninsula, and also in Africa.

The Ophiocephalidæ or serpent-heads are related to the Anabantidæ, and have a similar distribution, but more restricted in Africa, where they occur only in the west central region. They also possess an air-breathing organ, but of a much simpler structure. It is in fact merely a cavity on each side in front of the gills and communicating with the gill-cavity: the membrane lining the cavity is full of blood-vessels and is thickened and folded, but there are no bony plates connected with the gill-arches. There are only two genera, *Ophiocephalus* and *Chauna*, the latter without pelvic fins. They are found both in rivers, "tanks," and swamps, and are able to exist for considerable periods out of water and to travel over land: they also remain torpid or "æstivate" in the mud of dried-up ponds in the hot season. They are said by the natives to descend with downpours of rain, which is not impossible if they are taken up with the dried mud by violent whirlwinds. When living in muddy water they rise to the surface at intervals to obtain air.

The Osphromenidæ, although placed by Boulenger in the Spiny-finned Sub-Order (Acanthopterygii) while the Anabantidæ are considered to belong to the Percesoces, have considerable resemblance to the climbing perches. Like the latter they are fresh-water fishes of south-eastern Asia, and Africa. The Paradise-fish, *Macropodus viridi-auratus*, is a domesticated variety of the Chinese *Polyacanthus*, belonging to this family. Most if not all these fishes have labyrinthine organs like those of the climbing perch.

In the cat-fishes, *Clarias* and *Heterobranchus*, the air-breathing organ has the form of much-branched highly vascular out-growths of the dorsal ends of one or two branchial arches, enclosed within a posterior and dorsal chamber opening out of the gill-cavity. *Clarias* and *Heterobranchus* are again fishes of the Asiatic and African regions. *Clarias* has an elongated eel-like shape, and in Senegambia "æstivates" in burrows from which it emerges at night to crawl about for food.

*Saccobranchus* is another cat-fish of India and eastern Asia

which has a special air-breathing organ. (Plate XXXII., B.) In this case the organ is a long sac extending along the side of the body from the first gill-cleft to the tail. The sac is situated in a deep internal position close to the back-bone. The right sac is supplied by a branch of the first afferent branchial artery, the left by a branch of the fourth, and the wall of the sac is highly vascular. These sacs therefore resemble lungs and have a similar function, but open into the gill-cavity not into the gullet. The fish lives for days out of water.

*Amphipnous* is a fish allied to the eels and of similar elongated shape, without either pectoral or pelvic fins, and even the vertical fins are rudimentary. The air-breathing organs consist of a pair of bladder-like sacs opening from the branchial cavity above the first gill-cleft. The true gills are in this fish much reduced, the first arch having no gill-filaments, all its blood going to the air-sacs. There are only three branchial arches altogether, and the second alone bears gill-filaments. The fish, known familiarly as the cuchia, is, like most of these already mentioned, an inhabitant of the fresh and brackish waters of India and Burmah. It grows to two feet in length. It rises to the surface of the water to inspire air, and spends much of its time out of water in the grass on the banks of ponds, like a snake.

It was formerly a very general idea among zoologists that the lungs of higher vertebrates were evolved from the air-bladder of fishes. There is very good reason for regarding the two structures from the point of view of comparative anatomy as homologous, which means that they correspond to each other when we compare the general plan of structure of a fish with that of an animal breathing air by means of lungs. The explanation given by the doctrine of evolution of homology in such a case is that one of the two structures compared has been evolved from the other, or that both have been evolved from the same structure in some common ancestral form which lived at a former period. The progress of knowledge, however, has led to the conclusion that the air-bladder was evolved from lungs rather than vice versa. This may at first seem a paradox, but it does not mean that fishes are descended from terrestrial animals, and when we examine the evidence we shall see

that it is the most probable explanation of the facts. There was a natural tendency in the earlier days of the study of evolution to regard existing animals as forming a series corresponding to the series of steps in the evolution, and to overlook the fact that forms now living side by side, although some may retain more of the primitive and ancestral features than others, cannot actually be in the relation of ancestors and descendants. Thus although terrestrial vertebrates are doubtless descended from ancestral fishes, we cannot conclude that a mammal such as the dog is descended from a fish like the gold-fish, or that the lungs of the dog are a modification of the air-bladder of the gold-fish, which is not a respiratory organ, but an organ for decreasing the specific gravity of the fish.

Lungs are paired structures opening out of the ventral side of the oesophagus: the air-bladder in the majority of fishes is a single structure opening, when it is not closed completely, from the dorsal side of the oesophagus. But we must endeavour to trace the origin and history of the air-bladder in fishes themselves by the kinds of evidence usually employed by the evolutionist, by palaeontology, or the evidence of fossils, by comparative anatomy, and by embryology or the evidence of development. It is known that the fishes with closed air-bladders, classed together by Dr. Günther as Physoclisti, and comprising in Boulenger's classification the Spiny-finned Fishes (*Acanthopterygii*) and a few other Sub-Orders, are the latest fishes to appear in the palaeontological record, and in all these the air-bladder arises in development as an outgrowth of the gullet, the communication with the latter being afterwards lost. The Soft-finned Fishes (*Malacopterygii*) and a few other Sub-Orders, forming the old group *Physostomi* which retain, e.g. the salmon and carp, the communication of the air-bladder with the gullet throughout life, are therefore more primitive, and their fossil representatives are found in older geological strata. As the Spiny-finned Fishes are characteristic of the sea, so the Soft-finned Fishes for the most part live in fresh water, or are like the salmon and the eel inhabitants of fresh water during part of their lives. True Malacopterygians begin to appear as fossils in the chalk, forms closely allied to the smelt (*Osmerus*) and the anchovy (*Engraulis*), being known from this formation. The Holostei, of which the American bow-fin and bony-pike (*Amia* and *Lep-*

*idosteus*) are the living representatives, show in their fossil forms a complete transition to the Order Teleostei, which includes the great majority of existing fishes, and are undoubtedly their immediate predecessors and progenitors. Both *Lepidosteus* and *Amia* are confined to fresh water, and in both of them the air-bladder is single and opens into the gullet dorsally: at the communication there is a special chamber called the vestibule which resembles a larynx, the organ containing the opening to the lungs in higher Vertebrates, and communicates with the gullet by a narrow slit, the glottis. Moreover, in these two fishes but especially in *Lepidosteus*, the inner surface of the bladder is much increased by being produced into lateral recesses called alveoli, and each recess is again subdivided or sacculated much in the same way as in a true lung. In both of these fishes it has been shown by the American naturalist Wilder that the bladder is actually used for respiratory purposes.

In the Chondrostei or Sturgeons, the respiratory character of the bladder is not so apparent, the lining membrane is smooth, and the bladder opens without a vestibule into the dorsal wall of the pharynx. The fossil forms related to them are very old, Palæoniscidæ being represented in the Devonian, but most abundant in the Carboniferous and Permian strata. Of the living forms, the spoon-bill sturgeons are confined to large rivers, but the common sturgeons, though they spawn in fresh water, descend to the sea between the breeding seasons.

Thus we come to the fringe-finned ganoids (Crossopterygii) and lung-fishes (Dipnoi), which, as we trace them back to the beginning of their palæontological history, become difficult to distinguish from each other, and lead to the earliest bony fishes from which all the other groups have descended. The Crossopterygii as already mentioned are represented by only two living genera, *Calamoichthys* and *Polypterus*, inhabiting the great rivers of Africa, the Nile and the Niger. In *Polypterus* the air-bladder is divided, but the two parts are not symmetrical, that on the right side being long and tubular, while that on the left is much shorter, only about one-fourth the length of the other. The two sacs unite together anteriorly, and open by a single aperture into the *ventral* side of the gullet, like a pair of lungs. Mr. Budgett observed in specimens kept alive in captivity that air was inspired and expired through the spiracles, which are

present in *Polypterus*, although the inner surface of the bladders is not sacculated as in *Lepidosteus*.

In the living lung-fishes the respiratory function of the air-bladder is of course quite obvious, and in this respect they are intermediate between fishes and Amphibia. In *Ceratodus*, the Australian lung-fish (Plate XXXII., A), only one sac is present which lies above the intestines and extends from one end to the other of the body-cavity. The sac is large and wide, and along the median line dorsally and ventrally are two fibrous bands projecting into the cavity. Transverse bands passing between these on either side form the borders of two series of lateral chambers, which are again divided by projections of the wall into smaller alveoli, so that the respiratory surface is much increased as in a lung, and the wall is richly supplied with blood-vessels. The pneumatic duct, corresponding to a trachea or windpipe arises from the anterior end of the bladder on the right side, passes to the right of the gullet, and opens into the latter by a slit on the *ventral* side a little to the right of the middle line. We may conclude therefore that the whole bladder in *Ceratodus* is only the bladder of the right side, that of the left, which is smaller in *Polypterus*, having entirely disappeared.

In the African lung-fish *Protopterus*, and the South American *Lepidosiren*, the air-bladder although single anteriorly is completely divided posteriorly for the greater part of its length, but even in these the gullet does not pass between the right and left sacs, but the air-duct passes to the right of the oesophagus and opens into the ventral side of the latter. The structure, however, is so symmetrical that it is scarcely possible to regard it as formed by the division of a single sac like that of *Ceratodus* belonging to the right side: it appears rather as a median divided outgrowth of the gullet which has passed to the side of the oesophagus and become dorsal in position.

We have seen that the lung-fishes instead of being recently evolved modifications of the fish tribe are shown by their fossil remains to be exceedingly ancient. It might be suggested that although they themselves are ancient they have only recently evolved lungs, or recently begun to use the air-bladder for respiratory purposes. The earliest fossil forms, however, possess many of the special characters which distinguish the living lung-fishes from other fishes, such as the lobate paired fins,

and the large dental plates, and there is no reason to believe that the surviving forms have undergone a great change in the structure or function of the air-bladder. The most ancient lung-fishes were in some respects more similar to the fringe-finned ganoids (*Crossopterygii*) than their living descendants, and we have seen that the living *Crossopterygii* also use the air-bladder for respiration. It seems therefore the most probable hypothesis that this was its original function in these most ancient known bony fishes, and the reason for its evolution. No trace of an air-bladder is present in fishes of the shark type (*Elasmobranchii*) or in *Cyclostomes* (*Lamprey*, etc.), both more primitive types than the bony fishes (*Teleostomi*). In fact, we may suppose that the original fishes, more or less similar to sharks and dog-fishes, were inhabitants of the sea, where the water being saturated with oxygen there was no need of any atmospheric respiration to supplement the action of the gills. Some of these original fishes ascended the rivers and became inhabitants of fresh water, as some selachians and rays ascend the Amazons at the present day. Some of these forms made their way into streams or lakes where, from the hot climate and the decomposition of vegetable matter, oxygen was deficient and they began to swallow air at the surface to compensate for the failure of aquatic respiration. This appears from the evidence to have been the origin of the air-bladder, and at the same time, of the *Teleostome* type. From these air-breathing *Teleostomes* at a very early stage arose the earliest *Amphibia*, and on the other hand they multiplied in all the fresh waters, until some of them again reached the sea, where the air-bladder lost entirely its respiratory function and became a swim-bladder.

Although, however, it is probable that the air-bladder was primitively respiratory, it is by no means easy to explain its mode of origin. This question is intimately connected with the relations of the blood-vessels, arteries and veins, of the air-bladder to the heart, and these will therefore be described in discussing the question. The mode of origin which naturally suggests itself first is that the paired air-bladders were modifications of a pair of posterior gill-sacs of the kind seen in *Elasmobranchs*. This view was proposed in connection with the evolution of *Amphibia* as long ago as 1875; it assumes of

course that the gill-sacs are lateral outgrowths of the pharynx, which open by a superficial opening to the exterior. Goette, however, who proposed this theory, maintains that such pharyngeal gill-sacs, lined by hypoblast, *i.e.* by a continuation of the cells lining the pharynx, occur only in Cyclostomes, *e.g.* the lamprey, and in Amphibia, while the gill-sacs of Elasmobranchs are lined by a continuation of the layer of cells covering the external skin. In Teleostomes the gill-septa being reduced to narrow bars, there are no pharyngeal gill-sacs. Goette, therefore, supposes that the paired air-bladder arose in primitive fishes, and that the Elasmobranchs were derived from these before this structure had been evolved. This is a view which other zoologists do not accept, for there seems no reason to doubt that the gill-sacs of Elasmobranchs are outgrowths of the pharynx.

There is little evidence, however, either in the development or in the blood-supply of the most primitive air-bladders to support the view that these structures are modified gill-sacs which lost their opening to the exterior. If this view were correct we should expect that in an early stage of development at least the air-bladder of each side would receive an afferent branchial artery on the ventral side, and that its efferent vessel would be an efferent vessel on the dorsal side. There is no such arrangement known. In the Dipnoi, in *Polypterus*, and in *Amia* the air-bladder receives on each side an artery which is a branch from the fourth efferent branchial artery (epibranchial) as it does in the development of the lungs in terrestrial vertebrates. In Dipnoi the veins from the bladder open into the left auricle of the heart which is almost completely separated from the right, as in Amphibia: the connection is, therefore, behind the ventricle, not, as in gill-sacs, in front of it. In *Polypterus* the veins from the air-bladder join the hepatic veins, that is between the liver and the heart; in all other bony fishes they open for the most part into the hepatic portal vein, behind the liver, while some of them join the posterior cardinal veins; the arteries are derived from the dorsal aorta.

It has recently been denied that even in Amphibia the lungs in development correspond to gill-sacs, and stated that they arise as paired outgrowths in a more ventral position. In *Polypterus* whose development has recently been studied,

they begin as a widely open median groove, on the ventral side of the pharynx, and this outgrowth as it extends backwards divides into two horns, which almost from the first are unequal in length. The development in Dipnoi has yet to be studied.

Thus on the whole whether originally dorsal or ventral it seems most probable that the air-bladder had nothing to do in its evolution with gill-sacs, but was an outgrowth of the gullet or stomach, behind the heart, between this organ and the liver. If air was swallowed for respiratory purposes it would seem most probable that it would cause a dilatation of the dorsal side from its tendency to ascend. In any case as a part of the alimentary canal behind the gills, the bladder would naturally receive its arteries from the dorsal aorta or dorsal branchial arteries, and the evidence of *Polypterus* and the Dipnoi is in favour of the ventral connection with the gullet being the more primitive.

Among Teleostei with open air-bladders there are some cases in which the respiratory function of the organ is retained, and in fact the majority of the fresh-water forms at least seem to have the power of respiration air to some extent, as we see in the common gold-fish. Species of *Erythrinus*, one of the Characinae, living in fresh waters in Brazil, were found by Jobert to die of asphyxia if the pneumatic duct were ligatured. The same result occurred also in *Sudis gigas*, one of the Scope-lidæ.

The hydrostatic function of the air-bladder, that is to say its effect on the buoyancy of the fish, especially in the sea where there is a great range of depth, involves some interesting physical principles which are not generally appreciated. Every one knows that when fishes are caught and brought to the surface even from depths of only a few fathoms, the air in the bladder expands to such a degree that the stomach of the fish is often pushed out through the mouth. When the pressure on a gas is diminished by a half, the gas expands till its volume is doubled: at a depth of only five fathoms in the sea, the pressure on a fish is double the atmospheric pressure on the surface, and increases by one atmosphere for every five fathoms of depth. It is easy, therefore, to understand the great force of expansion exerted by the gas enclosed in the air-bladder when a fish is suddenly brought to the surface. The effect of the air-bladder

at any depth when the fish is alive and in normal condition is to render the weight of the fish equal to that of the water which it displaces : in these circumstances the fish has no tendency either to rise or sink, and can therefore keep at the same level in the water without any muscular exertion. A shark or dog-fish, on the other hand, having no bladder is heavier than the water and always has a tendency to sink ; it can only keep up by the action of its tail and fins. If, however, the fish with an air-bladder swims to a higher level, the gas in the bladder expands, the fish as a whole becomes larger and therefore lighter than the water it displaces, and has a tendency to rise more and more rapidly till it reaches the surface. Conversely, if a fish with an air-bladder swims to a slightly greater depth the bladder is compressed, the fish as a whole becomes smaller and heavier than the water displaced, and tends to sink with increasing velocity to the bottom. Such a fish in fact is in the condition of the scientific toy known as the Cartesian diver. This consists of a hollow figure containing a bubble of air which cannot escape because the aperture is at the lower end. The figure is placed in a tall jar of water over the mouth of which is fastened an air-tight cover of india-rubber or other flexible membrane. If the figure is so adjusted that it floats just at the surface of the jar, very slight pressure on the cover causes it to sink to the bottom and when the pressure is removed the diver rises again. It is easy by adjusting the pressure of the finger on the membrane to keep the figure in the middle of the depth of water. The pressure is transmitted to the air within the figure and compresses it so that it displaces less water and therefore the figure and the air together become heavier than the water. It is evident then that the air-bladder confines the fish to a very restricted range of depth, and it would be liable to float to the surface or to sink to the bottom at the slightest movement if it were not able to counteract the effect of changes of pressure by muscular compression or relaxation of the bladder or by increasing or diminishing the amount of gas in the bladder. This power, however, it can only exercise within narrow limits, and if suddenly brought to the surface it is quite unable to descend again. Fish caught to be kept alive in an aquarium are often, though otherwise uninjured, in this condition and float helpless at the

surface. By pricking the air-bladder with a needle through the side of the body some of the air is allowed to escape and then the fish recovers and may live for an indefinite time, whereas if left to itself it would very soon die.

It is evident from the above that an air-bladder would be unnecessary to a fish which lived on the ground, and a positive disadvantage to fishes which require to change rapidly from one depth to another. Accordingly we find that in ground-fishes the air-bladder is wanting, having disappeared in the course of evolution. It is entirely absent in the Pleuronectidæ or flat-fishes, in the Cyclopteridæ which cling to rocks by means of their suckers in shallow water, and in many of the littoral Blenniidæ. Its absence in many of the Scopelidæ seems to be related to the habit of these phosphorescent fishes of coming to the surface at night and sinking to considerable depths during the day. In the mackerel some species like the common British species have no air-bladder, and others possess one, although it is never very large; these are active predaceous fishes which change their depth very rapidly.

The gas contained in the air-bladder has been analysed, and found to consist of oxygen and nitrogen with a trace of carbon dioxide. These are the same gases as exist in the atmosphere, but the proportion of oxygen in the air-bladder is much greater than in atmospheric air, and is greater in marine fishes than in fresh-water forms, and greatest of all in certain deep-sea fishes. It has been maintained by Dr. Thilo that the gases in the bladder are originally derived from the atmosphere, and are simply swallowed by the fish, but this could not apply to the adults of those forms in which the bladder is closed, although it would be possible in their young stages, before the closing takes place. There are, however, certain structures known as red bodies and red glands in the wall of the air-bladder which contain a net-work of blood-vessels, and there is good evidence that these secrete gases and exude them into the bladder, while another structure known as the oval is believed to absorb some of the gas when necessary. The red bodies are modifications of the primitive general vascular supply in the walls of the bladder, the blood-vessels having become concentrated in limited areas, instead of being generally distributed.

The red bodies are situated on the ventral surface of the

bladder, and receive their blood supply from a branch of the coeliac artery, the corresponding vein joining the portal veins so that the returning blood passes with the blood from the digestive organs to the liver. In fishes with closed bladders, for example the maigre, *Sciæna aquila*, the red body consists of a dense collection of capillaries, above which is a thick mass of epithelial glandular cells: the vascular layer belongs to the inner of the three layers which form the wall of the bladder, the origin of the glandular mass is not known. Above the organ extends the layer of flat cells which everywhere lines the bladder. In *Sciæna* the glandular mass contains rounded cavities communicating with the surface by narrow channels: in other cases the glandular mass is thinner, and contains no cavities. According to Jaeger and Dr. Woodland to whom we owe the most important of recent investigations of the subject, the gland obtains oxygen from red blood corpuscles brought by the capillaries, and excretes it with some force into the bladder. This is the explanation of the fact that the pressure of the oxygen in the bladder is so much greater, especially in fishes which live at considerable depths, than what is called the tension of the gas in the blood.

The sense-organs are necessarily adapted to their special functions, and in fishes they present some very curious modifications.

According to the American zoologist G. H. Parker, there is no conclusive evidence that the sense of hearing exists at all in the majority of invertebrate animals, such as coral polyps, jelly-fishes, worms, star-fishes, crabs, oysters, snails, etc. These animals possess organs which resemble auditory organs, and were formerly so described, but recent experimental researches have shown that their function is the sense of equilibrium, a sense which is associated with the auditory organ in the vertebrates also. The only animals in which the sense of hearing is known with certainty to be present are the higher arthropods, especially the insects, and the vertebrates. The fact that the sense is certainly most developed in the animals which live in air suggests the question whether the sense really exists in aquatic animals, and in the case of vertebrates this question must be tested by the investigation of the sense in fishes. Bateson, from his observations at Plymouth, found that the re-

port or shock of the explosions made in blasting operations of rocks in the neighbourhood were followed by sudden movements in conger, flat-fishes, and pouting; while other fishes seemed to take no notice of the reports. When the side of the tank was struck by a heavy stick similar movements were produced. Pollack, however, made no response to the vibrations produced by striking a piece of glass with a stone under water provided the objects used were not visible to the fish. Bateson concluded that fishes perceive the *sound* of sudden shocks and concussions when sufficiently severe, but do not hear the sounds of bodies struck in the water but not perceived by them.

In several cases it has been stated that gold-fishes or other fresh-water fishes kept in ponds have been in the habit of assembling for food at the sound of a bell, which would be sufficient to prove not only that they possessed a sense of hearing but that they could hear sounds produced in the air and transmitted to the water. The Viennese physiologist Kreidl concluded from his experiments on the gold-fish that it made no response to sounds produced either in the air or in the water but only reacted, as Bateson found, to the shock of a blow given to the sides or top of the aquarium. He further removed the auditory nerves and the attached ear-sacs from several specimens and found that they reacted to shocks in the same way as uninjured fish. He concluded therefore that the fish does not perceive vibrations by the ear at all, but only perceives strong vibrations by the skin; the ear, according to this result, would only be concerned with the sense of equilibrium and direction which is one of its functions in ourselves. Kreidl investigated a special case of the assembling of fishes at the sound of a bell, namely the trout of a particular basin at the Benedictine Monastery of Krems in Austria. He found that the trout assembled equally at the sight of a person when no bell was rung, and if the bell was rung by a person whom they could not see the trout took no notice. If, however, a pebble or a piece of bread were thrown into the water the fish swam to the spot where the water was disturbed. Kreidl, therefore, maintained that the fishes were only affected by the sense of sight and the sense-organs of the skin. The American physiologist Lee made similar experiments and obtained results entirely in agreement with those of Kreidl. These results are,

however, difficult to reconcile with the fact that many fishes not only produce sounds but have special organs for its production, and that in some cases the voice is limited to the males as in the squeateague, *Cynoscion regalis*. These sounds are not of the kind which the experimenters above-mentioned found to be perceived by the skin. Accordingly G. H. Parker carried out a further investigation of the subject in America. He used an aquarium of which one end consisted of a deal board and confined the fish under experiment in a small cage in the middle of the aquarium, the side of the cage towards the sounding-board being closed only by a fine net. Outside the sounding-board was stretched a bass viol string giving forty vibrations per second. The fish chiefly used for the experiments were specimens of the killifish, *Fundulus heteroclitus*, one of the marine Cyprinodonts common on the east coast of the United States. Comparisons were made between normal fishes, others in which the auditory nerves had been divided, and others in which these nerves were intact and the skin had been rendered insensitive by division of the spinal cord. When the string was set in vibration the fishes responded by movements of the pectoral fins and by other movements. It was found that entire fishes regularly responded to the sound, and also those in which the sensibility of the skin was destroyed but the auditory nerves were intact, while those in which the auditory nerves had been destroyed gave no response. On the other hand, Parker was unable to obtain any evidence of the perception of true sounds in the smooth dog-fish, *Mustelus canis*. Zenneck in Germany found that three fresh-water species of fish, namely, the roach, the dace, and the bleak, showed distinct evidence of the perception of sound vibrations. At Parker's suggestion Bigelow repeated the experiments on the gold-fish, on which species Kredl had obtained only negative results. Bigelow used as source of sound a tuning-fork vibrating one hundred times per second and used great precautions to eliminate all other shocks or disturbances in the experiments. He found that the fish responded to the sound by characteristic movements, and gave the same response even after the auditory nerve of one side had been cut, but when both nerves were cut the responses disappeared.

In a large number of fishes the air-bladder has remarkable

special connections with the organs of hearing, so that the fish seems to make use of the physical properties of gases in the perception of sound as well as in its production. In this respect the fish, though living in a liquid, has greater resemblance to terrestrial animals than we might expect, for in ourselves and other vertebrates which live in a gaseous medium the tympanum or middle ear is an air-chamber which is accessory to the organ of hearing, and the voice is produced by the movement of air from the lungs.

There are three different modes in which the air-bladder is connected with the auditory organ. In many marine fishes the bony capsule surrounding the auditory organ on each side has an aperture closed by a membrane, and a tubular outgrowth from the air-bladder comes into contact with this membrane on the outer side, while on its inner side is the liquid surrounding the membranous labyrinth of the ear, the liquid called the perilymph. This arrangement occurs in certain species of the Gadidæ or cod family, and in the Serranidæ, Berycidæ, Sparidæ or sea-bream family, and the Notopteridæ. All these families belong to the spiny-finned fishes or Acanthopterygii, except the last, which is Malacopterygian, or soft-finned. In the second mode the apertures in the bony capsule of the ear are open, and the ends of the tubular extensions of the air-bladder are in direct contact with outgrowths of the membranous auditory vesicle. This occurs in the herring and pilchard and other species of the same family. In the third method the air-bladder is not directly in contact with the bony capsule or the auditory vesicle but is connected with the ear by a series or chain of small ossicles. These bones, known from their discoverer as the Weberian ossicles, are derived from the first four vertebræ, of which they are separated and modified portions. The ossicles are named claustrum, scaphium, intercalarium and tripus, on each side. The scaphium is inserted into the wall of the auditory capsule, and the tripus into the dorsal wall of the air-bladder at its anterior end.

The possession of the latter complicated apparatus is a common character of the Cyprinidæ or carp family, the Siluridæ, the Gymnotidæ, formerly known as the electric eels, and certain other families, which are consequently united by Mr. Boulenger in the sub-order Ostariophysii, for, as he points out,

such an agreement in the structure of so complicated and special an apparatus can only be the result of descent from a common ancestor. All these families are fresh-water fishes with open air-bladders and soft fin-rays, and therefore belong to the more primitive Teleostei in their general characters, although this particular adaptation is anything but primitive. It has been suggested that the close connection between the air-bladder and the auditory organ may have nothing to do with hearing, but may serve to enable the fish to perceive the variations of pressure in the air-bladder due to ascent or descent in the water. Even without the aid of consciousness or voluntary action, sensations of this kind might be related to reflex action affecting the blood-glands which as we have seen regulate the amount and pressure of oxygen in the bladder. It seems more probable, however, that the secretion and absorption of oxygen are regulated automatically by the pressure itself, and the connection of the air-bladder with the ear would be then really of auditory function. This view is supported by the fact that the fishes which possess Weberian ossicles are all inhabitants of rivers, or at least of fresh water, in which the range of depth is not very great, and such fishes may be held to be more in need of a delicate sense of hearing, than of special adjustments of the size of the air-bladder, or of the pressure of the gases within it.

It has long been agreed that the lateral line organs are sense-organs, but it has been always very difficult to discover to what particular stimulations they were sensitive. There is no evidence that they are affected by light, heat or electricity. Experiments have been made to decide whether the organs responded to chemical stimulation, such as oxygen, the salinity of the water, the dissolved substances of food, etc., but the results were negative. Mr. G. H. Parker has recently carried out a systematic series of experiments on these organs at the Government Biological Laboratory at Woods Hole, Massachusetts. The fish which he principally used was *Fundulus heteroclitus*, which is known in America as the killifish or mummichog, but experiments were also made on seven other species, including the smooth dog-fish, *Mustelus canis*, a skate, *Raja erinacea*, and a flat-fish, *Pseudopleuronectes americanus*. The method of experimenting was to cut the nerves supplying the lateral line and

also the fifth and seventh nerves supplying the similar organs on the head, and then to compare the behaviour of fishes so treated with uninjured specimens. Only one kind of stimuli were found to produce definite effects which were wanting in the fishes in which the nerves had been cut as described; these stimuli were vibrations of low frequency produced by pulling the aquarium slightly to one side and then letting it go. The rate of vibration was about six per second. Normal specimens of *Fundulus* when put into the aquarium swim first to the bottom, and after a time when they have become accustomed to their new surroundings they ascend to the surface. Any slight disturbance such as a quick movement of the observer or a slight jar to the aquarium causes them to descend to the bottom. The slow vibration above described has always the same effect. Specimens in which the nerves to the lateral line organs have been cut, on the other hand, take no notice of such vibrations, although they were sensitive to ripples on the actual surface. Similar reactions to the same kind of vibrations were observed in the other species of fishes tested.

On the other hand, it was proved that the lateral line organs were not sensitive to sound vibrations although the ears were. It has often been suggested that the lateral line organs are stimulated by currents in the water. All the fishes above mentioned in the normal condition were found to turn their heads always towards the direction of the current, but they did this with equal certainty after the nerves to the lateral line organs had been cut, so that apparently the reaction to the stimulus of a current of water depends on the ordinary tactile sensibility of the skin. The most important question arising from these experiments is: what are the stimuli which affect the organs in the natural life of the fish, and this question is not very satisfactorily answered by Parker. He found that when he produced strong ripples on the surface of the water by blowing upon it specimens of *Fundulus* invariably went to the bottom, while those whose nerves were cut only sank below the superficial water. Still more distinct was the reaction when an object unseen by the fish was dropped into the water. It seems to me from this that the chief use of the lateral line organs is to perceive the movements of other fish in the water. We do not know at present to what distance vibrations due to such movements

would extend, but it is evident that if a fish is affected by a body falling in the water it must also perceive the movement of another fish or animal in the water. We know that some fishes seek their food by sight and some by smell, but experiments have yet to be made to ascertain how far a fish without sight or hearing would be able to perceive the presence of an enemy in its neighbourhood.

The lateral line organs are originally developed on the surface of the skin, the tubes are formed by the closing in of a groove, and communicate with the surface by a series of pores. The tubes of the head, both the continuous ones of Teleostei and the separate ones of Elasmobranchs, are developed in the same way. In many fishes groups of sensory cells like the sense-organs of the lateral line occur on the free surface of the skin, for instance in the cod; and in addition to this the skin has doubtless a general tactile sensibility due to nerve endings not connected with special sense-organs. Experiment has shown that the skin of fishes is sensitive not merely to the contact of solid bodies, but also to the motion of the water in surface waves and currents. A normal fish usually places itself with its head towards a current and swims against it; it does this instinctively or automatically, and it can be easily understood that it must habitually do so in order not to be at the mercy of every current it meets. Parker found that a fish in which the lateral line nerves had been cut swam against a current in the same way as a normal fish and also swam downwards out of the reach of surface waves; it was evident therefore that the waves and the currents were perceived by the general skin without the aid of the lateral line organs.

The lateral line and the sensory tubes on the head form a single system of sense-organs radiating from the region of the auditory organ.

There is good reason to believe from embryological researches that the lateral line sense-organs were originally in ancestral fishes confined to the region of the branchial clefts, one organ belonging to each cleft; and also that the auditory organ is homologous with these organs, is in fact one of the series which has been specially developed. The auditory organ develops in the same way as the lateral line organs as an invagination of the surface of the skin. We do not know that

the branchial sense-organs were originally adapted to the perceptions of vibrations of the water, but we may regard the ear and the lateral line organs as exhibiting different degrees of modification of the same kind of sense-organ, and in their present state they are sensitive to vibrations of different frequencies. The auditory organ is thus a lateral line organ which has become more highly developed and adapted for the perception of the delicate vibrations of sound.

One of the most extraordinary adaptations of the eyes of fishes is that of *Anableps tetraphthalmus*, which are divided into two parts, the upper adapted for vision in the air the lower for vision in water. The eyes are large, and projecting across the surface of the transparent front part called the cornea is a horizontal pigmented band, the pupil is divided by a corresponding partition formed by anterior and posterior projections of the iris, and it is said that the curvature of the lower half of the lens is more convex than that of the upper part. This horizontal division of the eyes is exactly in line with the dorsal surface of the fish which is perfectly straight, and is exactly level with the surface of the water as the fish swims. (Plate XXXI., B.) This fish inhabits the rivers and estuaries of Central and South America, and its habits are thus described by an observer: They swim always at the surface of the water and in little schools arranged in platoons or abreast. They always swim headed upstream against the current, and feed upon floating matter which the current brings them. A platoon may be seen in regular formation breasting the current, either making slight headway upstream or merely maintaining their station, and on the *qui vive* for any food the current may bring. Now and then one may be seen to dart forward, seize a floating particle and then resume its place in the platoon, and thus they may be observed feeding for long periods. They are almost invariably found in running water well out in the stream, or at least where the current is strongest and where floating matter is most abundant, for it is upon floating matter that they seem chiefly to depend. They are not known to jump out of the water to catch insects flying in the air or resting upon vegetation above the water surface, nor do they seem to feed to any extent upon small crustaceans or other portions of the plankton beneath the surface. Rarely do they attempt to dive or to get beneath the surface; when they

do they have great difficulty in keeping under and soon come to the surface again.

The development of the eyes in this fish has been described in the Chapter on breeding, where it was pointed out that the peculiarities arise by a secondary change after the eyes are developed in the normal fashion, although the special structure is attained before the young are born. It must be admitted that we cannot at present show exactly how the conditions of vision following from the habit of surface swimming could in the individual tend to cause the changes in the eye which have taken place, but it is difficult to avoid the conclusion that these changes have been the direct result of the position of the eye to which they so exactly correspond. Other explanations should be able to produce some evidence of their probability, and there is no evidence of the occurrence of such modifications of the eye except in the fish which habitually swims with its eye half out of water. If the modifications only occurred under the conditions to which they are adapted, the conditions must be logically considered as the cause of the modifications, not by selection but by direct influence. *Dialommus*, a marine blenny from the Panama region, has its eye horizontally divided in a similar manner, and seems to have habits similar to those of *Anableps*.

In several species of fish the eyes are absent, or so rudimentary that vision is impossible. As in other animals this degeneration of the organs of sight occurs in fishes which live in darkness, and the case has attracted much interest among biologists in connection with the question of the evolution of adaptations: by one school of evolutionists the facts are considered to afford support to the belief in the direct action of conditions on the organism, while those who deny the possibility of the inheritance of acquired characters maintain that the loss of the eyes can be explained by variations or mutations which were independent of the external conditions. The most celebrated blind fish is *Amblyopsis speleæ* which lives in the stream flowing through the Mammoth Cave of Kentucky. This fish is not only eyeless but colourless, both conditions being either directly or indirectly the result of the absence of light. *Amblyopsis* is closely allied to the Cyprinodontidæ, and was formerly placed in that family. Several other species are, however, now known

which closely resemble *Amblyopsis*, and they are separated from the Cyprinodontidæ as a distinct family, Amblyopsidæ, differing from the former chiefly in two characters, namely that the mouth is scarcely at all protractile and that the anus is placed far forward close to the gills. The pelvic fins are rudimentary or absent, but this is also true of some Cyprinodonts. The family consists of three genera, *Chologaster*, *Typhlichthys* and *Amblyopsis*. In the first of these both eyes and pigment are well developed. *Chologaster cornutus* is abundant in the Dismal Swamp of Virginia and other swamps and rice-fields southward to northern Florida. It is less than two inches long, is destitute of pelvic fins, and is striped with longitudinal bands of black colour. *Chologaster papilliferus* is found under stones in the rivulets of Illinois, and *Chologaster agassizii* occurs in the underground streams of Kentucky and Tennessee. *Typhlichthys* is closely allied to *Chologaster* but is blind and colourless; it lives entirely underground in the limestone caves of southern Indiana, and thence southward to the north of Alabama. The fact that *Chologaster agassizii* is coloured and has well-developed eyes, although it lives in the dark, doubtless is sufficient to convince some biologists that the loss of eyes and colour in *Typhlichthys* is not due to the absence of light; but the fact is as puzzling on the selection theory as on the other. It is difficult to believe that constant residence in the dark does not at least reduce the pigmentation of *Chologaster agassizii* in the individual without any reference to heredity, but in any case it is obvious that *Typhlichthys* has become blind and colourless in consequence of living in the dark. It is probable that *Typhlichthys* has been subjected to the conditions of subterranean life for a much longer period than *Chologaster agassizii*, and that the latter will lose eyes and colour in course of time if confined generation after generation to a subterranean habitat.

*Amblyopsis spelæa* differs from *Typhlichthys* in its greater size, reaching a length of 5 in., and in the possession of small pelvic fins; thus although there can be no doubt that *Typhlichthys* is a modified form of *Chologaster*, which has lost eyes and colour in consequence of its subterranean life, the normal or ancestral form of *Amblyopsis* is unknown. It is confined to the east side of the Mississippi; in caves to the south of the Ohio both *Typhlichthys* and *Amblyopsis* occur together, to

the north of that river *Amblyopsis* occurs alone. The sense whose delicacy compensates for the absence of eyes in the blind fishes seems to be the sense of touch, or rather we should say the sensitiveness of the skin to vibrations. As in the Cyprinodontidæ, no lateral line is externally visible in the Amblyopsidæ, but whether the tube with its sense-organs is entirely absent is not stated. The surface of the skin is covered with sensory papillæ which are possibly of the same kind as the sense-organs of the lateral line and serve instead of the latter. Professor Cope, from observations on *Amblyopsis* in its natural habitat, stated that if not alarmed they come to the surface to feed and look like white aquatic ghosts, that they could then be easily taken by the hand or by net, provided no noise was made, for their sense of hearing was very acute, and at the slightest sound they swam down and hid beneath stones at the bottom. Miss Hoppin, on the other hand, found from observations on *Typhlichthys* in captivity that it was insensible to noises made in the air but immediately darted away if the side of the vessel was struck or if the water was disturbed or if the fish itself was touched. This seems to show that the fish was specially sensitive to the stimuli which Parker found to be perceived by the lateral line organs in *Fundulus*.

With regard to the evolution of the blind cave-fishes, the development of the blindness in the individual must be admitted to have an important bearing on the question of its origin in the species. The Amblyopsidæ, like the Cyprinodontidæ, are viviparous, and the development of the eyes in the embryo has been carefully investigated by Eigenmann. The young are born at a length of about half an inch, or 12 to 13 mm. The eye develops as an outgrowth from the brain at the same stage of growth as in normal fishes, when the embryo is 1.5 mm. long, but grows little after its appearance. The lens develops when the fish is 2.5 mm. long, but never loses its embryonic character, it soon degenerates and disappears altogether when the fish is 10 mm. in length, that is before birth. The retina and other parts of the eye have entirely degenerated by the time the fish is 13 cm. or about 4 in. and its highest stage is reached when the fish is 10 mm. long. This history of the eye is, at least in the opinion of the present writer, more in harmony with the view that the blindness is due to the gradual

effects of the absence of light, than with the view that it arose from spontaneous variations; certainly the gradual degeneration in the embryo is in no way similar to the sudden variations which are called mutations, which develop directly.

Whether by means of the positive selection of individuals with regressive variations of eyes and pigment, or as some maintain by the mere cessation of selection, or by the direct effect of the absence of light, subterranean conditions of life have produced similar results in fishes of different families and also in invertebrates. A blind and colourless crayfish lives in the underground waters of Kentucky and neighbouring states with the blind *Amblyopsis*. In caves of Pennsylvania there is a blind species of cat-fish called *Amiurus* or *Gronias nigrilabris*, closely related to species of *Amiurus* which are common in the rivers on the surface of the earth in that region. In caves of Cuba species of an entirely different family have become adapted to the absence of light: the Cuban cave-fishes belong to the genera *Stygicola* and *Lucifuga* of the family Zoarcidæ, and are evidently derived from marine ancestors, since they are the only fresh-water species of the family. Many of the Zoarcidæ live near the shore, and it is easy to understand how specimens might be carried by storms, or might make their way of their own accord, into the waters of caves, and survive there. These fishes, like *Brotula*, their nearest marine relative, have long dorsal and ventral fins confluent with the tail-fin. It is curious that one of the Cuban cave-fishes, namely *Lucifuga*, like the Amblyopsidæ, is viviparous, but this is not the result of subterranean conditions, since in both cases members of the same family living under ordinary conditions are also viviparous.

It is certain that the conditions of life in the deep abysses of the ocean are not similar, at any rate with regard to the absence of light, to those of subterranean caves, for abyssal fishes are not generally blind. In fact, there are very few deep-sea fishes which are totally blind, for example *Ipnops*, *Typhlonus*, *Aphyonus*, and *Tauredophidium*; of these all except the first belong to the family Zoarcidæ.

The habit of seeking concealment under stones or in crevices is characteristic of this family generally, and the loss of the eyes in the three abyssal members mentioned must be at-

tributed rather to such habits than to the conditions of abyssal life in general. The presence of eyes in other deep-sea fishes, these organs being often not reduced but enlarged, indicates the presence of light, which is believed to be produced by the luminous organs of the fishes themselves and of other animals. The blind species were obtained from depths between a thousand and two thousand fathoms in the Pacific and Indian Oceans. Garman has also described a species *Leucicorus lusciosus* from a depth of nearly two thousand fathoms in the Pacific in which the eyes are rudimentary and apparently functionless, iris and pupil being absent and the eyeball collapsed ; this fish also belongs to the Zoarcidæ. The condition of *Ipnops* and its relation to the Myctophidæ have been described in the section on phosphorescent organs ; eyes in this fish have apparently disappeared without leaving a trace, as there is no evidence to confirm the suggestion that the supposed phosphorescent organs are modified eyes.

Among the abyssal fishes discovered in the expedition of the *Investigator* in the Bay of Bengal, Alcock describes a deep-sea angler named *Onirodes glomerosus* with rudimentary eyes covered by the skin : it is only about 2 in. long, and is one of the species in which the dorsal tentacle carries a luminous organ. It came from 1260 fathoms. He also obtained a blind skate, *Benthobatis moresbyi*, dredged at 430 fathoms off the Travancore coast : the eyes in this species were too much reduced to be of any use, yet it had a row of luminous organs along the edge of the body. What can be the use of light to a blind fish ? Probably it serves to attract small fishes or other animals which serve as food.

The only other fish, besides the cave-fishes and deep-sea fishes mentioned, which is totally blind, is a species named *Typhlogobius californiensis* ; this is a small goby from 2 to 3 in. in length, said to be most nearly allied to *Crystallogobius nillsonii*, a transparent small fish which is common at depths of about thirty fathoms off the British and Irish coasts. *Typhlogobius* is found only in holes in the mud under stones at Point Loma, San Diego, California : the holes are excavated by a burrowing shrimp which lives in them in company with the fish. Both the animals are of a similar pink colour but the shrimp is not blind. It is a curious fact that according to Professor Eigen-

mann the same shrimp is found all over the Bay of San Diego and is accompanied by other species of goby such as *Clevelandia* and *Gillichthys*; but these fishes live outside the holes and only retreat into them when frightened, while the blind species is found only at Point Loma and never leaves the burrows of the shrimp. In this case therefore the relations of *Typhlogobius* and the other gobies of the neighbourhood are similar to those of *Typhlichthys* and *Chologaster* among the freshwater fishes of the Mississippi region, and it seems more probable that *Typhlogobius* is allied to *Gillichthys* or some other species of the same locality than to *Crystallogobius*. In fact, it is difficult to avoid the conclusion that the blind goby is simply one of the ordinary species of the district which has lost its eyes and pigment in consequence of its subterranean habits.

The development of *Typhlogobius* has been investigated and it has been found that, as in the blind cave-fishes, the eyes and pigment are much more developed in the young than in the adult, degeneration taking place subsequently. In the embryo of *Typhlogobius* within the egg the eyes and the pigment cells in the skin are developed exactly as in any ordinary species; in young specimens about  $\frac{1}{6}$  in. long the eyes are still externally visible, the membranes of the fins are thin and the skin is pigmented, the movements of the fish are also quick and active. In the adult the eyes are visible as minute specks, but are covered over by thick skin, the membranes of the fins are thick, the skin is without pigment, and the movements are sluggish; the adult fish is, however, extremely tenacious of life, surviving for a long time in vessels of foul water in which all other animals have died. Anatomical investigation shows that the eyes of the adult are covered by a thick layer of skin while the sclerotic or proper capsule of the eye is thin and connected with the surrounding fibrous tissue; the lens is present and spherical but the cavity behind it is collapsed and the retina is rudimentary; the optic nerve is very minute and the eye-muscles rudimentary. It is evident that the eyes are functionless.

With regard to the skin, microscopic examination showed that the pigment was not entirely absent in the large specimens. The pigment is situated on the inner surface of the skin, the thickness of which in the adult fish is much increased and which is also very richly supplied with blood-vessels. It

seems, therefore, that the pink colour is not due merely to the loss of pigment but is caused by a positive development of blood-vessels in the skin, which doubtless perform the function of cutaneous respiration ; the supply of oxygen in the holes in which the fish lives must be considerably reduced, since there is no free movement of water through them, and thus we can understand that it is advantageous or even necessary to the fish that the ordinary respiration of the gills should be supplemented by absorption of oxygen through the skin. The cave-fish *Amblyopsis* lives in running water in which there is no dearth of oxygen, and accordingly, although its pigment has disappeared in consequence of the absence of light, its skin is not specially vascular and its colour is not pink but white. The cutaneous respiration of *Typhlogobius* explains its power of living in foul water in captivity.

In all the gobies the sensory tubes of the lateral line and head are wanting and the sensory organs of the head are on the free surface of the skin. It has been suggested that in *Typhlogobius* the reduction of the eyes is compensated by the higher development of these dermal sense-organs, but W. E. Ritter found that such organs were less numerous in the blind species than in more normal forms. In *Typhlogobius* there is a series of sensory papillæ parallel to the lower jaw, another series on the upper jaw and another on the operculum, but on the sides of the body sense-organs are entirely wanting ; in the species possessing the sense of sight these series on the head are present and there are also others scattered on the head and numerous transverse series on the sides of the body.

A very extraordinary condition of the eyes occurs in *Stylophthalmus paradoxus*, a deep-sea fish of the Indian Ocean : the organs are at the ends of long slender stalks projecting from the sides of the head. The stalks become shorter in the adult fish.

## CHAPTER IX

### ADAPTATIONS (*CONTINUED*)

#### PRODUCTION OF SOUND, LIGHT AND ELECTRICITY

Voice of fishes. Stridulating organs. Fishes which possess luminous organs. Microscopic structure of luminous organs. Electric fishes. Structure of electric organs. General remarks on evolution.

OUR knowledge of the voice of fishes is not very complete for several reasons. Although water is an excellent conductor of sound, the vibrations do not pass easily from the water to the air, and an investigator cannot well remain under water while he is making experiments on the subject. Sounds are therefore usually heard when the fish emitting them is taken from the water, and then there is often some doubt whether it is accidental or is produced by special muscular action in the normal life of the fish. There are, however, many cases in which there is no doubt about the voice, or the special mechanism by which it is produced, and the majority of these cases occur among the Teleostei. One of these of which the present writer can speak from personal experience is that of the sapphirine gurnard, *Trigla hirundo*, known among the North Sea fishermen as the tub or latchet. This fish emits distinct sounds which may be described as a succession of short grunts. The sounds are produced by the air-bladder, and the mechanism was investigated by the French naturalist Moreau in 1864. The air-bladder is divided by a transverse diaphragm perforated by a hole in the centre; the diaphragm itself contains radiating and circular muscle-fibres, and the bladder has thick strong external muscles of the striated or voluntary kind, supplied by two large nerves from the anterior part of the spinal cord. The diaphragm, according to Moreau, is thrown into vibration by air being forced from one compartment of the bladder to the other through the aperture. Some of the other

species of gurnards are said to produce sounds, but although the bladder generally has powerful external muscles the diaphragm does not seem to be always present. The John dory utters similar sounds. The maigre (*Sciæna aquila*) has attracted attention in all ages, especially in the Mediterranean, for the loud and varied sounds it makes. The voice in this case is sexual in function, and is chiefly produced in the breeding season, when the fish are in shoals. It has been suggested that the ancient Greek myth of the song of the sirens arose from the sounds uttered by the maigre, but it may be doubted whether human imagination required any such aid in the evolution of fairy tales. Another species of the same family as the maigre, the "drum" (*Pogonias chromis*) has a more muscular air-bladder and produces louder sounds. Like the latter it is an inhabitant of the tropical and subtropical parts of the Atlantic, and its drumming is heard chiefly in the spawning season.

The exact mode in which sound is produced in the two families to which these fishes belong (*Sciænidæ* and *Triglidæ*) has quite recently been successfully explained by the researches of Tower in America. In the former family there is a specific sound-producing muscle, the *musculus sonificus*, which is not directly attached to the bladder but arising from the wall of the abdomen on each side, passes upwards to a central tendon which lies above the air-bladder; the muscle is red in colour. The muscle is thrown into a series of contractions at the rate of twenty-four per second, and these throw the abdominal walls and organs, but especially the air-bladder, into vibration. When the bladder was removed or deflated the sound ceased but it was produced again when an artificial bladder of india-rubber was introduced, which proves conclusively that though the sound proceeds from the bladder it is caused by the muscle and that the bladder does not itself set up the vibrations. In *Micro-pogon* the sound is produced by both sexes, in *Pogonias*, the drum, *Cynoscion*, the squeateague, *Leiostomus*, and *Bairdiella* it is produced only by the males: Tower found that the *musculus sonificus* was present only in the males of these latter genera but in both sexes of *Micropogon*. The sound uttered by these *Sciænidæ* is described as a drumming noise, that is to say it is a continued booming sound such as that produced by beating rapidly on a drum. In the gurnards, on the other hand, the

sound is a single short grunt which may be repeated but is not a continuous sound. In these fishes it was shown that the sound is produced by intrinsic muscles in the wall of the air-bladder, and a grunt is caused by a single contraction of these muscles; it can be called forth by electric stimulation even in a bladder which has been taken out of the fish. The sound was not produced when the bladder was deflated, but returned when a rubber bladder was put inside the natural one so that the diaphragm is not necessary. In *Opsanus tau*, the common toad-fish of the American coast, the mechanism was the same as in the gurnards (Triglidæ).

The bladder functions as a vocal organ not only in marine but in many fresh-water fishes, for instance in several South American cat-fishes (Siluridæ) and Characnidæ. The blind fish of the Mammoth Cave of Kentucky is not also dumb but calls its mates and companions by sounds, and the same power is possessed by *Lucifuga*, the blind fish of the subterranean waters of Cuba, although the former species has an open air-bladder and is allied to the Cyprinodonts, while the latter has a closed bladder and is allied to the Blennies.

In *Doras* and several other genera of South American cat-fishes there is a special adaptation for the production of sound consisting of an elastic spring mechanism by which the wall of the bladder is thrown into vibration. The springs are formed of the elongated transverse processes of the fourth vertebra, the ends of which are expanded and attached to the wall of the air-bladder. Two powerful muscles pass from the skull to the springs, and the contractions of these muscles causes the springs and with them the walls of the bladder to vibrate rapidly and produce a sound.

In some fishes sounds are produced by the movement of air through the mouth or through the opening of the air-bladder, but it is not proved that such sounds are naturally emitted by the fish in its normal life. The conger is said by the fishermen to bark like a dog when it is caught, but this seems to be merely an exaggerated description of gurgling sounds certainly produced by the fish in its struggles to escape. The carp is said to produce a sound in the same manner.

It is curious to notice that the voice of fishes in the cases we have mentioned is not produced by vibrations of solid parts

of their bodies in their natural medium, namely water, but that the vibrations originate in connection with a gaseous medium and in fact are produced by the organ which is homologous with the lungs, by which the voice of terrestrial vertebrates is produced. There are, however, cases in which sound is produced, as in other aquatic animals, by structures entirely surrounded by water; this mode of producing sound is called stridulation, and stridulating organs occur in many Teleosteans. One of the most complicated organs of this kind is that of the Indian siluroid, *Callomystax gagata*; in this fish the dorsal spines of the third, fourth and fifth vertebræ are united together and articulated with the supraoccipital bone of the skull; the united spines form a high narrow plate of bone which is vertically divided behind by a cleft in which moves the first interspinous bone of the dorsal fin; the inner sides of the cleft and the outer sides of the interspinous bone are covered with close-set vertical ridges like those of a file, and these ridges rubbing against each other produce a harsh grating noise; the fifth and sixth vertebræ are joined by an unusually wide intervertebral ligament so that they can move upon one another freely and the stridulating organ is put into action by the bending of this joint up and down in the vertical plane, the ordinary lateral movements of the body having no effect upon it. Stridulation between different parts of the skeleton has been stated to occur in many species of fish and is probably used as an expression of emotion, but owing to the natural difficulties evidence of the actual and voluntary production of sound by the fish in its natural state is scanty or wanting. In some siluroids a process of the anterior spine of the pectoral fin stridulates against the wall of a socket in the pectoral girdle to which the fin is articulated. The spines of the dorsal fin are said to produce sound by friction against neighbouring bones in several trigger-fishes of the genera *Balistes*, *Monacanthus*, and *Triacanthus* in the boar-fish (*Capros aper*), and in the three-spined stickle-back. According to Dr. Otto Thilo, however, the peculiar articulations of the spines in these cases are examples of click mechanisms, the effect of which is to keep the spines erected without muscular exertion, as they can only be depressed when the click is removed, as in the mechanism of a clasp knife; such an arrangement probably produces a sound, at any rate in the

dead fish, but the sound is probably accidental and of no importance. In the drumming trigger-fish (*Balistes aculeatus*) which lives among the coral reefs of Mauritius, there is an apparatus whose sound-producing function seems beyond doubt. It consists, according to the German naturalist Möbius, in the movement of certain bones of the pectoral girdle against one another. Both these bones are in close contact with the air-bladder, and the walls of the latter are over a certain area in contact with the skin which is seen to vibrate when the sounds are being emitted. Here again, therefore, we have the air-bladder and its gaseous contents playing an important part in the production of sound.

The present writer recently had an opportunity of studying the production of sound in a species of trigger-fish, *Balistes buniva*, which is very abundant at the island of Ascension in the Atlantic. When the mail steamer on which the writer was a passenger anchored off the island, shoals of this fish gathered round the ship to feed on refuse thrown overboard, and from a boat at the foot of the ladder he was able to take a specimen alive with his hand. Just behind the pectoral fin is an area of the skin resembling a drum, a portion of the air-bladder being immediately beneath it: this drum is distinguished from the surrounding skin by being covered with large scales meeting edge to edge, not overlapping like the ordinary scales. When the drumming sound was produced the pectoral fin was moved rapidly to and fro and the membrane of the drum could be seen to vibrate. When the pectoral was forcibly kept motionless in a forward position by the finger and thumb, no sound was produced. It certainly seemed as though the sound was due to the vibrations of the drum itself, and as though these vibrations were due to the striking of the drum by the fin, but it was impossible to decide whether the friction of the internal bones of the pectoral girdle was necessary to produce the sound as Möbius states. There can be no doubt that the vibrations of the drum give rise to the sound, the only question is whether these vibrations are caused by the pectoral fin striking the drum externally, or by the friction of the bones internally.

Lastly, it may be mentioned that some fishes make sounds by grating together their upper and lower pharyngeal teeth. This has been proved to occur in the common scad or horse-

mackerel, *Caranx trachurus*, in the sun-fish, *Orthagoriscus mola*, and in a species of *Balistes* or trigger-fish : in the last case the sound is described by Moseley in the "Naturalists on the Challenger," as heard by himself when the living fish was held in the hand. I noticed the same thing myself at Ascension in a specimen of *Balistes vetula*, a large, brilliantly coloured species, common in many parts of the world. This specimen had a drum behind the pectoral fin and produced a sound from it like *Balistes buniva*, but it also produced a quite distinct sound from inside its mouth, and I have no doubt this second sound arose from friction between the pharyngeal teeth.

The luminous or light-producing organs in fishes which are best known and which have been known for the longest time are those of the Scopelidæ, or as the family is now called Myctophidæ. In these fishes the organs usually have the form of small pearl-like beads arranged in rows and groups on the sides of the lower half of the body, reminding one of the pearlies of a coster dandy. (Plate XXXI., C.) Several species of these fish are not uncommon in the Mediterranean and specimens taken there were described and named in 1810. A great number of species are now known both from the Mediterranean and from the Atlantic and also from the Pacific. The family belongs to the sub-order Haplomi, typified by the common pike. All the members of the family in the restricted sense of the name as here used have luminous organs or photophores. Many of the commonest species are taken on the surface of the ocean, but only at night; in the day time and in rough weather they descend to unknown depths. The range in depth of these fishes is one of the puzzles of Ichthyology. As they have an air-bladder, although it is small and has an open duct, it is difficult to understand how they can accommodate themselves at one time to the surface and at another to a depth of some hundreds of fathoms ; yet the records of oceanic expeditions often state that specimens of the same species have been taken at different times under these different conditions. The explanation in some cases at least is doubtless that a dredge or trawl worked on the bottom at a depth of a thousand fathoms or more may catch small fishes, not on the bottom, but at any point during its ascent to the surface. It seems very doubtful, until we get more certain evidence, that any fish can live both at the surface

and at a depth of a thousand fathoms. All the species of *Myctophum* may be regarded as pelagic and nocturnal fishes visiting the surface at night, but other species of the family are probably truly abyssal and never taken at the surface.

The Myctophidæ are small fishes not more than a few inches in length with a rather blunt snout and large eyes ; the pelvic fins, as in other open-bladdered fishes, are abdominal in position ; there is one rather large dorsal fin in the middle of the back, and behind this usually a rudimentary or "adipose" fin ; the tail-fin is forked. The small pearly organs are situated in a series on each side along the ventral edge, in groups on the sides near the lateral line, on the mandible, and on the operculum ; in addition to these there are in some species larger organs called sternchasers, on the dorsal edge in front of the tail and others in front of and below the eye.

In earlier times light-producing organs both in fishes and in invertebrates were supposed by some to be accessory eyes. Although this view can no longer be maintained, the emission of light by the living fishes has only rarely been observed. Dr. Günther was one of the first to see and describe light produced by these organs in a living *Myctophum* ; during a gale while he was in the Channel Islands he obtained a living specimen which was cast ashore ; the light was seen to proceed from the special organs ; it was irregularly intermittent, sometimes well defined like a round spark, sometimes more diffuse. It did not extend to the tail region which was probably already paralysed, and it ceased with the life of the fish. Mr. Guppy, on board H.M.S. *Lark*, took two specimens of a species of *Myctophum* near the Cape of Good Hope, one of which was alive ; the dead specimen displayed no luminosity even when irritated, but the one that was still alive showed faint but undoubted light in the pearly bodies of the pectoral region which were larger than the others ; the production of light was not affected by any irritation.

There is no close connection between the possession of luminous organs and the conditions of abyssal life : just as many surface fishes possess these organs, so many abyssal fishes are destitute of them, and so far as we know have no power of emitting light. Allied to the Myctophidæ, are numerous other fishes formerly united with them in the same family, some of

which occur at moderate depths, others at very great depths, and many of which do not possess luminous organs. For instance, in the whole family Synodontidæ there are no such organs. One of these named *Benthosaurus* was taken by the *Challenger* off the coast of New Zealand at a depth of 1100 fathoms, other specimens were taken by the American exploring vessel *Albatross* at similar depths. Another species of the same genus was taken by the *Challenger* at the enormous depth of 2385 fathoms in the South Pacific. On the other hand, *Harpodon nehereus* belonging to the same family is caught in great numbers for food in the estuary of the Ganges, and in the dried state is well known to Anglo-Indians as Bombay duck. It is stated to be brilliantly phosphorescent all over the body when first caught, but it has no special luminous organs. It is possible, as Dr. Günther says, that this fish usually lives at some considerable depth and only comes into shallow water temporarily, perhaps to spawn, for it has the sensory canals of the lateral line and head much enlarged as in most deep-water fishes. Another allied family, that of the Chlorophthalmidæ, which means green-eyed fishes, is also without luminous organs. *Bathypterois*, a member of this family, occurs off the coast of Brazil at 500 to 700 fathoms; it has the upper rays of the pectoral fins prolonged to a length nearly equal to that of the body and evidently serving as tactile filaments whose sensitiveness compensates for the small size of the eyes.

Perhaps the most extraordinary of all abyssal fishes is one called *Ipnops*. Placed by some ichthyologists among the Chlorophthalmidæ, by others in a family by itself, it is in all probability a truly abyssal fish. It was originally discovered by the *Challenger*, four specimens having been taken off the coast of Brazil and to the north of Celebes at depths varying from 1600 to 2150 fathoms. In this fish there are no small light-organs like those of *Myctophum*, but the head is flattened and the whole of its upper surface is occupied by a pair of peculiar organs believed to be phosphorescent, while eyes are entirely absent, and apparently the olfactory organs also. (Plate XXXI., D.) These organs in the preserved fish have the whitish, opaque appearance which is characteristic of luminous organs generally, but the actual emission of light from them has never been observed, the specimens taken being always dead by the

time they reach the deck of the vessel. The name *Ipnops*, meaning lantern-face, supposing that the organs are really light-producing, perfectly expresses the remarkable condition of this fish. The *Challenger* species was called *Ipnops murrayi* after Sir John Murray, one of the scientific staff on the *Challenger* at the time of its discovery and editor of the *Challenger Reports*. In 1891 another species was discovered in the Pacific by the American investigating vessel *Albatross* under the charge of the eminent American zoologist Alexander Agassiz and named after him; a single specimen about six inches long was taken from a depth of about 1360 fathoms off the west coast of South America.

The *Sternoptychidae* are another family in which luminous organs are developed to the highest degree and which have been taken frequently at the surface. *Sternoptyx diaphana* has been known since the year 1774 when a specimen was described from the West Indies. It was taken by the *Challenger* all round the world in the tropical seas, in the middle of the Atlantic, in Australian waters, and in the South Pacific. The *Challenger* records would seem to prove that this species lives at all depths from the surface to 2500 fathoms, but as Doctor Günther says this is very improbable and it is more probably, like *Myctophum*, not abyssal but pelagic, and only caught in deep-sea dredges or trawls as they ascend towards the surface. Like *Myctophum* also it comes to the surface at night. It is a small fish with short, deep body, much compressed from side to side. A series of light-organs runs along the lower part of the abdomen near the ventral edge on each side, another series on each side of the throat in front of the gill-opening, a row of three above and behind the base of the pectoral fins, and another row of three above the anus. On the tail there are two rows of four, anterior and posterior.

*Argyropelecus* (silver-axe, from its shape and silvery skin), another member of the same family, is also pelagic with highly developed luminous organs. It has been obtained in the trawl at 500 and 600 fathoms, but is frequently caught at night in the surface net. Giglioli in 1878 obtained over 700 specimens in three days at Messina where the currents and whirlpools bring all kinds of marine forms to the surface. A specimen was taken by the *Challenger* off Cape Finisterre at 1125 fathoms,

but was probably taken by the dredge on its way to the surface.

*Polyipnus* (many lanterns) is one of the most remarkable of this family, having no less than 55 luminous organs on each side. It was obtained by the *Challenger* at 250 fathoms between the Philippine Islands and Borneo, and by the Indian vessel *Investigator* at about 200 fathoms. It is not therefore an abyssal fish and probably not a bottom fish. Two species of the Sternopychidae have been taken on or near the British coasts. One of these, *Maurolicus pennantii*, is common in the Mediterranean ; it is a small slender fish more regular in shape and not so deep in the body as *Sternopyx* ; the sides are silvery and there are two row of luminous organs along the ventral edge. It has occurred most frequently on the north-eastern coast of Britain, not as might be expected on the south coast ; usually it has been cast ashore during storms ; in 1882 about 170 specimens were picked up on the beach at Aberdeen after storms in January, February, and March. It has also been obtained at the Orkneys, in Wick, in the Firth of Forth, at Redcar in Yorkshire, in Devonshire, at Weston-super-mare and off Flintshire, and in Ireland near Dublin. It is evidently a pelagic fish living near the surface and possesses little power of active swimming. Of the other species, *Argyropelecus hemigymnus*, only a single specimen has been taken in the British area, having been caught in the dredge by the *Porcupine* in 1869 at a depth of 540 fathoms between the Shetlands and the Faroe Islands. In the Mediterranean and the Atlantic it has been frequently taken at night at the surface.

The Sternopychidae belong to the sub-order of Soft-finned Fishes or Malacoptyergii, and the Stomiatidae are by Boulenger united with them in one family ; it is, however, more convenient to consider the Stomiatidae as a separate family. The majority of these fishes are undoubtly abyssal and are never taken at the surface. They are usually of elongated form with large mouths and formidable dentition, evidently of voracious and predatory habits, and they usually possess conspicuous luminous organs. One of the commonest of these fishes is *Chauliodus sloani* ; it has been long known from the Mediterranean and has been obtained from various depths from 500 to 2000 fathoms in the Atlantic and the Bay of Bengal. It has on each side a

row of phosphorescent spots near the ventral edge extending from the chin to the tail. *Astronesthes*, on the other hand, though in its long teeth and in the presence of a long barbel on the chin it has the characters of a bathybial and ground-haunting fish, has frequently been obtained at the surface, but it was also recorded by the *Challenger* from 2500 fathoms. It seems possible that true deep-sea fishes are occasionally carried to the surface in some way not well understood, and it is difficult in many cases to be sure whether a species is naturally pelagic or only occurs at the surface accidentally. *Astronesthes* has luminous organs in two rows along each side near the ventral edge, a luminous patch higher up on the side behind the head, two patches beneath the eye on the upper jaw and another central patch on the forehead. In 1854 the emission of light by living specimens of *Astronesthes* was twice observed by Professor Reinhardt. The specimens were captured at the surface in the Atlantic between 6° and 23° N. Lat., where they are fairly common and they gave out a strong and vivid greenish light which occasionally ceased for a moment and then reappeared. The fish soon died and then the light ceased altogether. Numerous species of the type genus *Stomias* are known; they have mostly been taken from depths of less than a thousand fathoms in the Atlantic, the Indian Ocean, and the Pacific. They are long, slender, snake-like in shape with large head and large mouth and teeth: they have a double row of luminous organs on each side as in *Astronesthes*, and a well-developed barbel on the chin.

*Malacosteus* is an extraordinary form with an enormous mouth, the gape extending backwards beyond the bases of the pectoral fins. There is a strong elastic cord attaching the tongue to the middle of the lower jaw to prevent rupture of the mouth by the large prey which the fish swallows. There is a large crescentic luminous patch below the eye and another a little farther back. The colour is black with minute white spots scattered over the body which may also be luminous. The *Challenger* specimen was taken at 500 fathoms near the Philippines; other specimens of closely allied species have been taken in the Atlantic at depths over 1000 fathoms. Another peculiar fish of this family is *Idiacanthus*, called *Bathyophis* by Günther. It is a very slender elongated fish with a somewhat enlarged head and mouth and a long barbel on the chin. It has a small luminous

organ above the edge of the upper jaw on each side and the usual series near the ventral edge of the body. One specimen was taken by the *Challenger* in the middle of the Atlantic at the depth of 2750 fathoms, but two specimens had previously been obtained at the surface to the north of New Guinea; in this case, however, there can hardly be any doubt that the fish is really bathybial and lives near the bottom.

The Alepocephali are a family of bathybial fishes allied to the Clupeidæ and Salmonidæ; some of the members are scaled and in most of these luminous organs are absent, but in the scaleless forms the skin, at least in some species, bears scattered small projecting nodules which have the appearance and structure of such organs. One of these species is called *Xenodermichthys nodulosus*, and a single specimen was taken by the *Challenger* south of Japan at a depth of 345 fathoms. *Aleposomus socialis* is another species of which large numbers of specimens were taken in the French expedition of the *Talisman* off the west coast of Africa at a depth of about 600 fathoms. It has spots, probably of the same nature as those of *Xenodermichthys*, on the head and anterior part of the body.

There is, however, some reason to conclude that deep-sea fishes may be luminous even when they possess no special light-organs. *Alepocephalus affinis*, for instance, taken from a depth of 753 fathoms off the Kistna coast in the Bay of Bengal, is described by Lt.-Col. Alcock as being quite black in colour and having its skin everywhere covered with a thick opalescent epidermis which was uniformly luminous; he states that the only specimen captured glimmered like a ghost as it lay dead at the bottom of a pail of sea-water. The glimmering of a ghost is not a phenomenon authenticated by any scientific evidence, but the observation that the surface of the fish glimmered although no special light-organs were present is of considerable scientific interest.

The Halosauridæ are fishes with strongly marked characters placed by Boulenger with the parasitic Fierasferidæ and a few other families in a separate suborder, the Heteromi. Their affinities are not very certain. They have a pointed snout projecting beyond the jaws, a single short dorsal fin about midway between snout and anal region, a long caudal region tapering to a point without distinct tail-fin, and a long

ventral fin. As the pelvic fins are abdominal in position they are doubtless allied to the more primitive soft-finned malacopterygian and open-bladdered fishes, but the air-bladder is stated to be closed. Some members of this family, all of which belong to the deep-sea fauna, are generally stated to possess luminous organs, but the organs supposed to produce light are very different in nature and structure from the undoubtedly luminous organs of other fishes, and there is no satisfactory evidence that these organs have anything to do with the production of light. In all other cases the light-organs are situated in various parts of the skin, are innervated by branches of the ordinary dermal nerves, and are not connected with the lateral line.

In Halosauridæ, the organs supposed to be luminous are on the lateral line and seem to be merely the proper lateral line organs enlarged. The organs of the lateral line are sense-organs supplied by branches of the lateral-line nerve, and it seems to be held by some zoologists that the sense-organs in this case have developed a light-producing function. Only three genera of Halosauridæ are recognised, and in two of these (*Halosaurus* and *Halosaurichthys*) the scales of the lateral line are not much enlarged and are stated to be destitute of luminous organs; in the third genus, *Halosauropsis*, of which there are several species, the scales of the lateral line are much enlarged and expanded, and are said to bear light-organs. The only reason for this statement seems to be that each scale of the lateral line in this genus is somewhat transparent and shows a conspicuous opaque white spot in preserved specimens, which is not visible in the other genera; but in several deep-sea fishes the tubes of the lateral line and sensory canals on the head are much enlarged and this is apparently due to the greater development of the dermal sense-organs under abyssal conditions. *Halosauropsis* lives on the whole at greater depths than the other two genera, and it seems most probable that the supposed light-organs are nothing but the enlarged sense-organs of the lateral line. The lateral line sense-organs, like other sense-organs, are connected with sensory, i.e. afferent nerves, along which nerve-impulses travel towards the brain. It is well known that nervous impulses pass along nerves only in one direction, an afferent or sensory nerve cannot become an efferent nerve.

Luminous organs, on the other hand, must be supplied by efferent nerve-fibres, along which impulses pass from the brain or spinal cord to the organs. Sense-organs, therefore, could never become luminous organs. It would be necessary to show that light in Halosauridæ is produced by glandular cells surrounding, but distinct from the sensory cells, and no attempt has been made to prove this, nor have the organs in question been seen to emit light. Specimens of Halosauridæ have been obtained in all the great oceans. *Halosauropsis* also possesses a white glandular patch on the skin behind the gills covered in the natural state by the operculum; it seems probable that this is really a luminous organ.

Among the Spiny-finned Fishes (Acanthopterygii) organs which can with certainty be regarded as luminous occur more rarely than in the more primitive forms above considered, although in various cases the function of producing light has been attributed on insufficient evidence to various structures in the skin. In many of the deep-sea forms, for example in the families Zoarcidæ or Brotulidæ, the dermal organs of the lateral line and head are much enlarged as in the Halosauridæ, and like the latter have been supposed, especially by American ichthyologists, to have a light-producing function, of which there is no direct evidence. Several oceanic or abyssal forms of the angler family (Lophiidæ) possess organs, of whose light-emitting function there can be little doubt, at the extremities of the dorsal filaments which are characteristic of the family. In these cases the light seems to serve as a lure to attract other fishes within reach of the angler's jaws. One of these forms is *Ceratias uranoscopus*, of which a specimen 9 cm. or nearly 4 in. in length was taken by the *Challenger* at a depth of 2400 fathoms between the Canary and Cape Verde Islands. The body is compressed and deep and the first spine of the anterior dorsal fin forms a long filament arising from the top of the head and nearly as long as the body: the filament terminates in a pear-shaped bulb at the outer end of which is a semi-transparent whitish spot, probably a luminous organ. *Cryptopsaras couesi* is a somewhat similar fish in which the bulb of the filament is larger and continued into a whitish thread. In *Melanocetus murrayi*, taken in the Atlantic at 1850 and 2450 fathoms, the dorsal filament is dilated at its extremity, but it is not certain that

it bears a luminous organ. Of *Linophryne lucifer* only a single specimen is known, which was picked up at the surface near Madeira by a sea-captain; it had swallowed a fish larger than itself: in this remarkable fish the cephalic tentacle is short and thick, black in colour and enlarged at its end into an ovate bulb the outer half of which is white and probably luminous. There can be no doubt that this fish naturally lives at the bottom in considerable depths; it has enormously long teeth and a long barbel below the chin. In *Caulophryne jordani*, taken in the Atlantic at 1200 fathoms, there is no luminous organ on the cephalic tentacle but numerous short luminous filaments scattered over the head and body; the second dorsal and ventral fins are much elongated and also the caudal fin.

In the genus *Porichthys* of the family Batrachidæ which is intermediate between Blennies and Anglers, the skin, which is scaleless, bears numerous series of small spots; these have been supposed to be pores of the dermal canal system, but it has been proved that on the body there are no sensory canals present, the sense-organs of the lateral line system being on the free surface of the skin. Some of the small spots are sense-organs of this kind, similar to those which occur in most fishes within the lateral canal, and consisting of little buds of epidermic cells connected with branches of the sensory nerves, while others have an entirely different structure, a structure which resembles that of phosphorescent organs. *Porichthys notatus* occurs abundantly along the Pacific coast of North America from Sitka to Panama. It is caught in spring and summer between tide-marks or in shallow water, where it comes to spawn. Its eggs are cemented in a single layer to the under surface of stones, and the male guards them, and takes care of the young brood until they are an inch in length. In surface view the phosphorescent organs appear as bright silvery spots or beads in the general brown coloration, the average number is 350 on each side of the body. Some of the lines of spots consist of phosphorescent organs only, in others these are associated with sense-organs, usually one phosphorescent organ being placed above, and one below each sense-organ. Mr. Greene kept specimens of the toadfish, as it is locally called, in aquaria and observed it carefully in the dark, both when it was quiet and when violently excited, but never saw any phosphorescence,

except once when the fish was pressed against the side of the aquarium, and a scarcely perceptible glow was observed. The fish lives on the shore, and is quite common, so that if it was phosphorescent in its natural state, the fact could scarcely fail to attract notice, but no evidence of light being observed to be emitted by the fish has ever been brought forward. On the other hand, it is certain that the organs are really light-producing organs, for when the fish was put into sea-water to which a little ammonia had been added, it exhibited a most brilliant glow of light along the lines where the organs were situated, and the individual organs were distinguishable as the sources of the light. The light appeared after five minutes, remained bright for a few minutes, and during twenty minutes gradually diminished almost to zero. Rubbing the hand over the organs was always followed by a distinct increase in the luminosity. Even pieces of the skin containing the organs cut from the fish five or six hours after it was dead, became luminous when treated with ammonia water.

The emission of light was also produced by electrical stimulation. When the electrodes of an induction coil were applied to the fish a brilliant glow of light was seen in every phosphorescent organ. These experiments were made on specimens taken from under the rocks where they were guarding the young brood. It is a curious fact that specimens taken by hook in deeper water could not be made to show any phosphorescence either by ammonia or by electric stimulation. It seems therefore that the power of emitting light is developed only in the breeding season, but there is no evidence that the power is ever exercised by the fish in its natural state. Evidently a special investigation of this point is required.

Among the most interesting and remarkable of all the luminous organs of fishes are those which occur in two small species of the East Indies, which were investigated by the Dutch naturalists on the voyage of the *Siboga*. These fishes are about 3 in. in length and appear to belong to the division Perciformes of the Spiny-finned sub-order. One of them, *Anomalops græffii*, has been obtained at Amboina, Fiji, Paumotu Archipelago, and the New Hebrides. Both of them are rather common at the Banda Islands, where they were studied by Professor Max Weber on the voyage of the *Siboga*. The

second species is named *Photoblepharon palpebratus*. The luminous organs in these fishes is a movable disc below the eye which can be withdrawn into the orbit and is then covered by a flap of skin like an eyelid, situated above the organ; when the organ is exposed the edge of the disc extends to the edge of the pupil so that the vision of the fish is not obscured and the light is prevented from passing through the coats of the eye by the dense pigment with which the inner surface of the organ is covered. The luminous organ is thus like a dark lantern placed immediately beneath the eye and the light can be exposed or covered at the will of the fish. When the disc is cut out from the head of the fish it retains its luminous power for several hours, and it is put on a hook and used as a luminous bait by the native fishermen, who are extremely ingenious and energetic. It has been supposed that these fishes were abyssal but this is not the case; *Anomalops*, called by the natives ikan leweri laut, swims in shoals at the surface of the sea; *Photoblepharon*, distinguished as ikan leweri batu, lives singly among the rocks. Obviously the luminous organ can only be of advantage as a bait in the dark, and in the living fish likewise the habits must be nocturnal.

The power of emitting light occurs also in some of the shark order, namely, in several species of the family Spina-cidæ to which our common spiny dog-fish *Acanthias vulgaris* belongs. As long ago as 1840 Bennett described the phosphorescence of a specimen of a species of shark or dog-fish called *Isistius brasiliensis* which he observed alive on a whaling-ship. The emission of light lasted for three hours, when the animal died and the light ceased. Bennett's description is as follows: "The entire inferior surface of the body and head emitted a vivid and greenish phosphorescent gleam, imparting to the creature by its own light a truly ghastly and terrific appearance. The luminous effect was constant and not perceptibly increased by agitation or friction. The only part of the under surface of the animal which was free from luminosity was the black collar around the throat; and while the inferior surface of the pectoral, anal and caudal fins shone with splendour, their superior surface, including the upper lobe of the tail-fin, was in darkness, as also were the dorsal fins, back and summit of the head." Another observer in 1860, also called Bennett, states

that in his specimen the light continued for some hours after death. Nearly all the specimens have been taken at the surface both in the Atlantic and Pacific, but the large eyes and dark or black colour suggest that the fish lives in the dark, perhaps coming to the surface only at night. *Spinax niger*, which is also black and lives in deep water in the Mediterranean, has been observed to be phosphorescent at the Zoological Station of Naples, and the production of light is due to numerous organs of simple structure.

We have now to consider the principal points in the structure of these light-producing organs and the question how the light is produced. The structure of the organs in different fishes so far as it has been investigated shows a great diversity, so that it is difficult at present to explain them as modifications of a common type. We will first describe the principal kinds and then consider whether any general conclusions can be drawn as to how the light is produced. All the organs are special modifications of the tissues of the skin, and therefore to understand them it is necessary to have some knowledge of the ordinary structures present in the skin. The skin consists of two layers, an outer called the epidermis consisting of several layers of cells without blood-vessels and an inner portion, called the derma which is thicker and is composed of felted fibres. The epidermis is almost transparent and soft so that it is easily removed by friction and in preserved specimens may be lost altogether. The scales are thin calcified plates, that is horny plates containing a certain amount of compounds of lime. The scales usually overlap one another, the outer edges being directed towards the tail of the fish, and the scale in front covering about three-fourths of the one behind it. It is a mistake to suppose that the scales are on the surface of the skin, they are in the derma beneath the epidermis, but the posterior edge of the scale may project to some extent through the epidermis. The derma is supplied with blood-vessels and nerves; it contains living cells in the meshes of the network of fibres; it also contains two kinds of structures which contribute to the coloration of the fish. These two kinds are first the pigment cells, some of which are black and others coloured, and second the reflecting elements which are called iridocytes. These elements of coloration are situated chiefly in the outer part of the skin below

the epidermis and on the surface of the scales, and in another layer on the inner surface of the derma. The dense white or silvery appearance of a fish is due to a thick and dense layer of iridocytes on the inner surface of the skin; this layer is called the argenteum. The substance of the iridocytes is quite opaque and has a very remarkable power of reflecting light: in some cases, as on the lower sides of flat-fishes, the surface of the argenteum is merely a dead white, but in a large number of fishes the reflection from the same layer is bright and silvery as in the salmon; in these cases the reflection is similar in appearance to that from a polished metallic surface or from mercury, although there is no metal in the reflecting substance of the fish. Lastly, in many fishes in addition to the silvery reflection there is a brilliant iridescence or play of colours, which is due to iridocytes scattered singly, not crowded together in a dense layer. The iridocytes consist of a special chemical substance identical with one which was first found in guano and which is therefore called guanin. Guano is the dried excrement of sea-birds which feed principally on fish, and the guanin in it is derived from the skins of the fishes eaten, this substance being so insoluble that it is not affected by the digestive processes, but passes through the birds' intestines unchanged. Owing to its beautiful lustre the reflecting substance of fishes' skins is used for the manufacture of artificial pearls. The species of fish from which the supply of the material is usually obtained on the continent is *Alburnus lucidus*, the bleak, a fresh-water fish of the carp family, which is common also in British rivers. French artificial pearls are made by coating the insides of glass beads with this substance, which is known in the trade as blanc d'ablette or essence d'Orient. Roman pearls on the other hand are made from the reflecting substance of the air-bladder of the Argentine, a marine fish of the salmon family; and this substance is not placed in glass beads but on the external surface of beads made of wax.

Among the various organs of fishes known or believed to produce light three different types of structure can be distinguished: first that which is found in the organs of Myctophidæ or Scopelidæ; second that of organs in other families which are not connected with the lateral line; third, that of the lateral line organs in Halosauridæ and other families.

1. *The Photophores of Scopelidæ*.—In these small pearl-like organs the essential or special body which appears to produce the light is a somewhat flattened circular disc composed of thin plates lying one over the other, nearly parallel to the

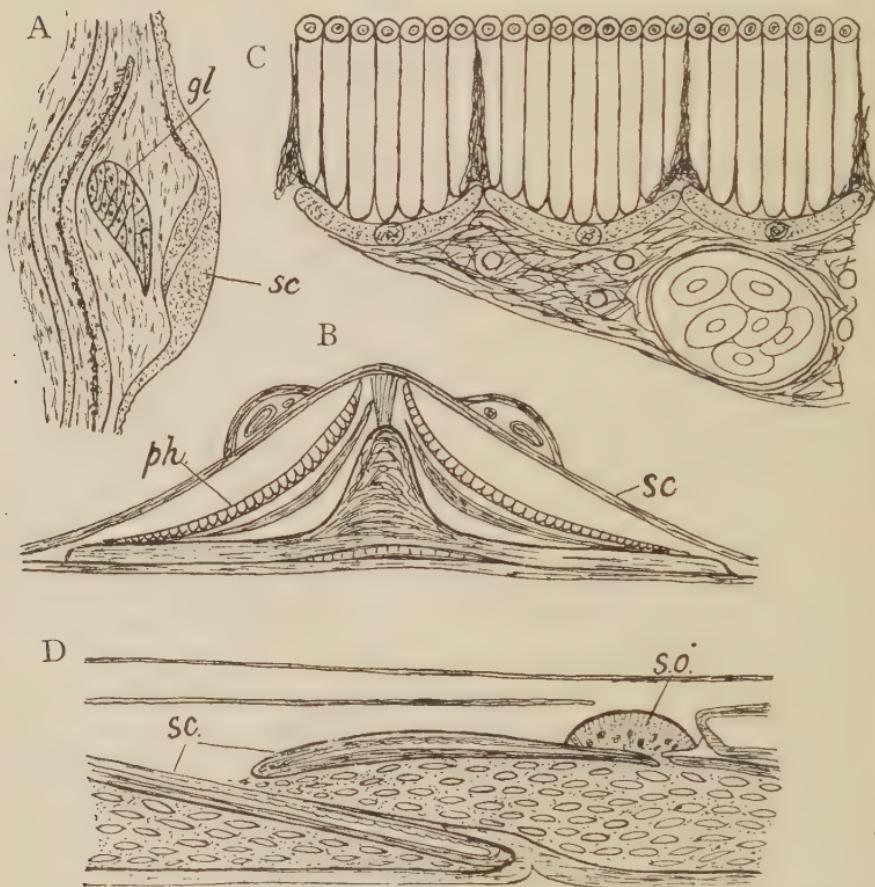


FIG. 30.—Microscopic Structure of Luminous Organs of Fishes. A, Section of pearl-like organ of *Myctophum*, after von Lendenfeld. B, Section of head of *Ipnops*, after Moseley. C, Portion of same more highly magnified. D, Longitudinal section of lateral line of *Halosauropsis*, after von Lendenfeld. *gl.*, gland; *sc.*, scale; *ph.*, phosphorescent organ; *s.o.*, sense-organ.

surface of the skin ; between the plates are nuclei. This special body lies between two overlapping scales, the outer of which is transparent and thickened to form a lens by which the light is concentrated. The inner scale is thin and concave and on its inner surface is covered with reflecting substance, internal to which again is a layer of pigment. The inner scale thus evi-

dently acts as a reflector and resembles a glass mirror, being backed by a silvery reflecting layer like the mercury at the back of the glass, and this layer being covered by opaque pigment like the opaque substance over the mercury.

Of the various theories which have been suggested concerning the process by which light is produced in the luminous organs of fishes and other animals, the most definite and probable is that the essential part of each organ consists of glandular cells, which secrete a substance containing phosphorus, that this substance is oxidised by oxygen supplied by the blood, and that the light is due to this oxidation. Our knowledge of the skin in general indicates that its glandular cells are usually derived from the epidermis, and that the cells of the connective tissue of the skin do not become glandular. In the organs of the Myctophidæ it seems difficult to apply this theory, firstly because the special organ does not appear to be composed of glandular cells, and secondly because it has been stated by Emery that this organ is developed in the derma and is not derived from the epidermis. Accordingly other investigators have maintained that the light is produced in these organs electrically; but this statement has little definite meaning, as no attempt is made to connect it with what we know of electricity in general; it seems to be based merely on the laminated structure of the special body which suggests the plates of an electric battery. On the other hand, the investigators last mentioned state that the special body is derived in development from the epidermis and not from the derma, and this if correct would be in favour of the glandular theory.

2. *The light-organs of Sternopychidæ, Stomiatidæ, etc.*—

These organs, although they differ greatly in degree of complexity, agree in the glandular character of the essential part of the organ by which the light seems to be produced. Modified scales take no part in the structure of these organs; they are provided on the internal surface with a reflector formed of the reflecting substance of the skin, *i.e.* of iridocytes, and this is covered by pigment cells; there is no definite single structure acting as lens, but the outer part of the organ consists of transparent refracting cells, whose function is believed to be optical. As examples of this type, we may take the organs of *Sternopyx* (Fig. 31). In this fish the lateral organs consist

of an inner part shaped like a rounded sac, and an outer part opening by a wide oblique aperture on to the surface of the skin: the two parts are separated by a constriction. Both parts are surrounded internally by, first, a layer of iridocytes forming the reflector, and, outside this, by a layer of pigment. The inner sac is filled with gland tubes, radiating from the mouth of the sac to the walls. The tubes are lined by large granular cells, which seem to pour their secretion into the cavity of the sac, especially towards the mouth. The contents of the outer part of the organ are quite different: here there are a number of short cylindrical or prismatic columns perpendicular to the surface of the skin. Each of these columns consists of a core of blood-vessels and nerves, surrounded by slender radiating cells some of which are enlarged at their outer ends, and contain a transparent refringent body. These cells have been supposed to be the special phosphorescent cells, but if the light is produced by the glandular cells of the inner sac, it would seem more probable that the cells of the outer portion are merely refracting structures. In the ventral organs of *Sternoptyx* which are to a great extent united internally, although the apertures of those of the two sides are separated by a median ridge, the external part does not contain columns like those above described, but appears to contain glandular tubes. It is evident that thorough investigation of fresh specimens of the fish is still required in order to ascertain with more certainty the functions of the different parts of the organs.

The two ventral rows of organs in *Astronesthes* are of two kinds, one larger, compound in structure, the other smaller and simple. The compound organs are somewhat similar to those above described in *Sternoptyx*; they consist of an internal spherical part separated by a constricted neck from an outer part shaped like a paraboloid cup with its aperture towards the surface of the skin. The spherical portion is divided by radiating lines into tubes containing glandular cells; the neck portion consists of two transverse layers of large cells; the outer cup is filled with a somewhat granular tissue in which radiating lines are distinctly visible; these lines are fibres radiating from the neck of the organ to its aperture; each fibre is surrounded by slender cells arranged like the hairs on the tail of a squirrel. It is possible that this tissue of the cup is refractive in function,

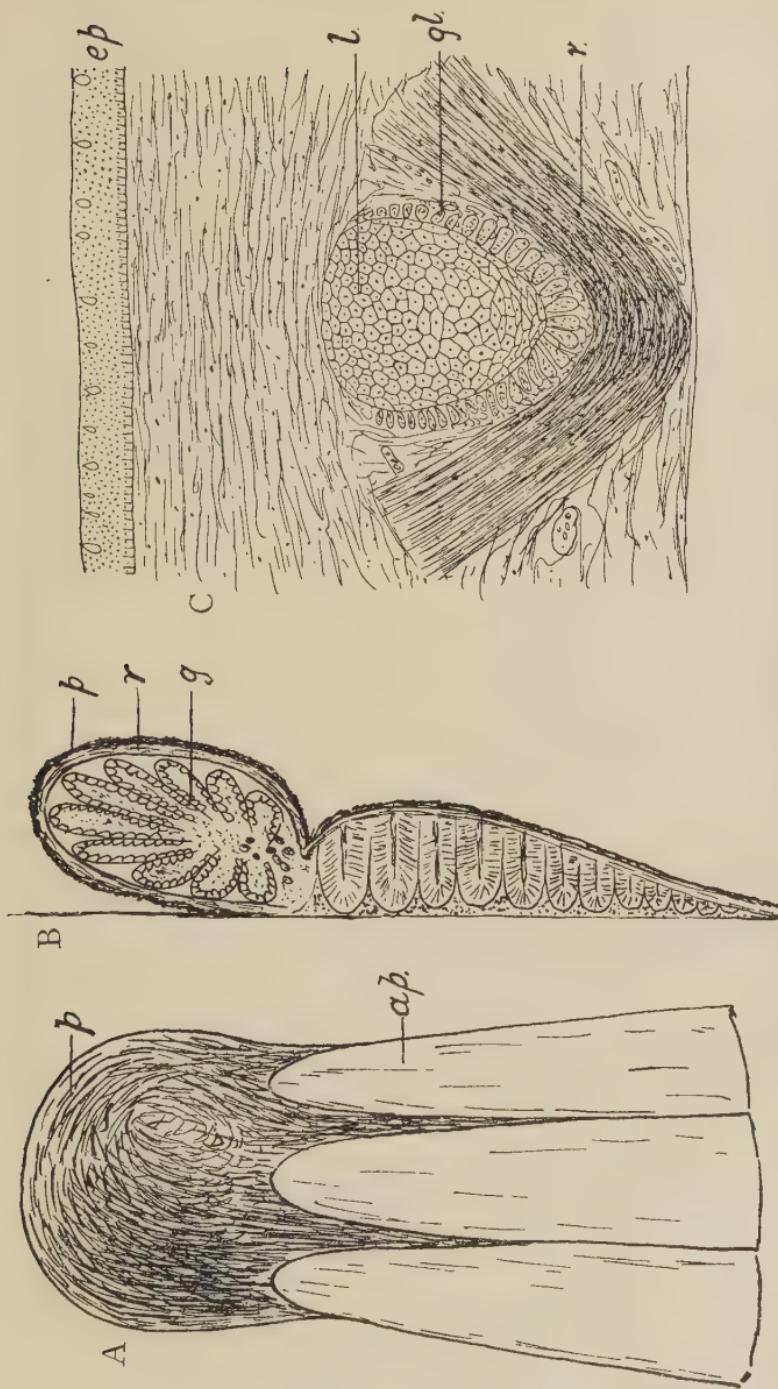


FIG. 31.—Microscopic Structure of Luminous Organs of Fishes. A, Surface view of the three partially united, postero-lateral organs of *Sternopyx diaphana*. B, Longitudinal section of same, after von Lendenfeld. C, Section of phosphorescent organ of *Porichthys notatus*, after Greene. *ap.*, aperture; *φ.*, epidermis; *g.*, gland; *l.*, lens; *r.*, reflector; *p.*, pigment.

condensing the light produced in the spherical inner part of the organ. The whole organ is surrounded by a layer of pigment cells within which is a thin reflecting membrane, much thinner than the reflector in the organs of *Sternoptyx* but probably of the same nature. The smaller simpler organs of *Astronesthes* are like the inner portion of the compound organ without the outer cup.

In many fishes there are luminous organs of larger extent and less regular shape than those above described. These usually consist of glandular tissue similar to that found in the inner parts of the compound definite organs; the suborbital organ of *Astronesthes* for example is enclosed internally by a thin light-reflecting membrane and outside this by a pigment layer, but there is no well-developed reflector. In other cases, as in *Pachystomias microdon*, the suborbital organs have a compound structure like that described in the compound organs of *Astronesthes*, but the organs are of greater superficial extent. The internal portion is glandular and is surrounded by a thick reflector. The surrounding skin extends somewhat over the margin of the organ, and it is probable that in the living fish the organ can be covered or exposed at the will of the fish, as is known to be the case in the little East Indian fish *Anomalops*, described above.

The projecting organs of *Xenodermichthys* are very different in structure from any yet described, but they are covered by pigment at the sides and not at the ends, and their internal tissue seems to contain gland-cells and refringent club-shaped cells like the more typical luminous organs.

It is obvious enough that the pigment and reflecting layer surrounding the luminous organs on the internal side are special developments of the ordinary pigment cells and iridocytes of the skin, but the origin of the essential tissue of the organs has not, in the organs hitherto considered, been described in detail; some Italian investigators, however, state that they have found in certain species of the *Stomiatiidæ* that the light-producing tissue is derived, as would be expected, from the epidermis. The most complete account we have of the structure and development of the various constituents of a phosphorescent organ is that given by the American investigator Greene for the organs of *Porichthys*, and although these are more rudimentary and, as

mentioned above, of more doubtful function than those we have already described, it is possible that the chief facts of structure and development established for them will be found to be true of the majority of others. The skin of *Porichthys* is destitute of scales, the epidermis is glandular, the derma thick. The phosphorescent organs are situated in the deeper part of the derma near its internal surface. Each organ (Fig. 31, C.) consists of lens, gland, reflector, and pigment, succeeding each other in the order mentioned from without inwards. The reflector is thick and is shaped like a conical cup with its aperture towards the surface of the skin : lining the cavity of the cup is a layer of large nucleated granular cells which have the character of gland-cells, though of course in this case, as in other luminous organs, there is no duct and the secretion does not escape to the exterior. The rest of the cavity of the cone is filled with a mass of smaller cells which are dense, homogeneous, transparent, and highly refractive ; this mass is the lens, but it has no smooth regular surfaces like the lens of an optical instrument or like that of the eye, its density and transparency cause it to refract and condense the light, but there is no need for a definite focus or for the formation of an image as in an organ of sight. The glandular layer is well supplied with blood-vessels. On the outside of the reflector there are some pigment cells. No nerve bundles or conspicuous nerves pass to the phosphorescent organs, they are merely supplied by small nerve fibres from the ordinary nerves of the skin. The development of these organs was completely traced out in young fishes ; the lens-cells and gland-cells arise as a thickening of the deeper or internal layers of the epidermis and the thickening forms a little mass of cells which grows inwards into the derma and then becomes separated from it, sinking into the substance of the derma where, on the base and sides of the mass, are developed the reflector and pigment layer, which are merely local developments of the iridocytes and pigment cells of the derma. The mass of cells derived from the epidermis differentiates into the lens-cells and gland-cells. Although the luminous organs are in many parts of the fish in proximity to the sense-organs of the skin, they have no connection with these structures, which also arise as special developments of epidermic cells, but they have quite a different structure and grow outwards to the surface of the epidermis not

inwards towards the derma. It seems very probable that all true luminous organs, at least all those of the second group, consist of gland-cells and lens-cells derived from the epidermis.

The curious organs on the head of *Ipnotops*, however, if they are really luminous organs, show no resemblance in structure to those of any of the three groups which we have distinguished, and must be considered separately. *Ipnotops* has no eyes, and it has been supposed that the flat white pair of organs on the head (Plate XXXI., D.) were really the eyes converted into luminous organs, but according to Moseley there is no evidence of this, as the organs have no resemblance to eyes and are not innervated by the optic nerves, which are entirely wanting. The olfactory organs and nerves are also rudimentary, but the auditory organs are well developed. The luminous organ on each side is situated between the surface of the cartilaginous skull below and a large flat scale above, running longitudinally, in which is a mucous tube apparently belonging to the dermal sensory system. The organ itself consists of a large number of six-sided columns placed vertically on the base of the organ. Each column appears white and glistening at its external surface and is separated from its neighbours by black pigment. It consists of 30 to 40 transparent rods resting inferiorly on a layer of pigmented tissue; beneath it is a single large six-sided pigment cell, and the outer extremity of each vertical rod is a six-sided nucleated cell. No distinct nerve connection was traced, but it seemed probable that the nerves passing into the organ from the subjacent fibrous tissue originated from the 5th cranial nerve. Moseley was of opinion that these organs were greatly enlarged representatives of the luminous organs in front of and below the eye in some species of *Myctophum*, these organs having united together and occupied the whole of the orbit, while the eye had degenerated. It is difficult, however, to compare any of the elements in the organs of *Ipnotops* with those of the more usual types of light-organ; it will be noticed that the reflector is entirely absent from the organs of *Ipnotops*. There is one type of organ which has been described in some Sternopychidæ and Stomiatiidæ which contains cells somewhat similar to the vertical rods of the organ of *Ipnotops*. These organs consist of a spherical inner portion and a conical outer portion like those of *Sternopyx* described above, but in the inner portion instead

of radial tubes or chambers containing gland-cells there are long single cells radiating from the wall of the spherical sac to its centre; these seem to be the light-producing cells, and it is possible that the vertical rods in *Ipnops* are of similar nature. On the other hand, the vertical columns of the organs of *Ipnops* present rather more resemblance to the columns of the electric organs of *Torpedo* than to any structures in luminous organs, and it seems possible that they are really electric organs formed by the modification of the muscular tissue of the orbits and anterior region of the head; but the columns are not described as consisting of superimposed plates like those of electric organs. Without further investigation nothing more can be said, and as the capture of specimens of *Ipnops* from the abysses of the ocean is a rare event we may have to wait a long time for any addition to our knowledge on the subject.

3. The phosphorescent or radiating organs of *Halosauropsis*, as described by von Lendenfeld (Fig. 30, D.), are nothing but the epithelial sense-organs of the lateral line and sensory tubes on the head. They consist of slender columnar cells placed vertically to the supporting membrane, and the organs have a free surface to the cavity of the canal; there is nothing in them resembling in any way the structure of luminous organs. Whether any of the accessory structures of the canals have a light-producing function it is impossible to decide; there is a peculiar tissue beneath the scales of the lateral line which contains numerous lens-shaped structures, and there are gland tubes around the canal, but of the function of these structures we have no evidence.

Phosphorescence is a property of numerous Invertebrates, and luminous organs as definite as those of fishes occur also in some of them, for example in certain Crustacea, but no animals except fishes are known to possess organs whose special function is to produce electricity. In certain fishes alone in the animal kingdom does the energy produced by vital processes assume the electrical form.

The electric powers of the *Torpedo* are generally known; the commonest species is *T. hebetans*, also called *T. nobiliana*, which is frequently taken on the south coast of England and occasionally on the other coasts of Great Britain and Ireland. This species and others of the same genus occur more abund-

antly in the Mediterranean, the Atlantic, the Red Sea, and the Pacific. Other members of the family, referred to different genera, occur in the tropical or subtropical seas all over the world; *Narcine* lives in the East Indies, Tasmania, China, Japan, South Africa, and the Atlantic coasts of America; *Discopyge* in the eastern Pacific, and *Hypnos* in Australian waters. In all the species the electric organs are present; they are situated on either side of the body between the anterior prolongations of the pectoral fins and the gills. These fishes in structure are similar to the common skates; they are flattened dorso-ventrally and live on the ground; as in skates, the pectoral fins are enormously enlarged and extend forwards to the front of the snout, but the edges of these fins are circular, not rhomboid as in the skates.

Somewhat rudimentary electric organs also occur in the skates and rays (genus *Raia*), but it is curious that these do not correspond to the organs in *Torpedo*, but are placed on each side of the terminal portion of the tail.

The other fishes in which electric organs occur belong to some of the more primitive families of the Order Teleostei. The so-called electric eel, *Gymnotus electricus*, is, as we have seen, not an eel at all but is the type of the Family Gymnotidæ which is allied to the carps and cat-fishes or Siluroids, while the eels belong to a different sub-order, the Apodes. *Gymnotus* (Plate XXXII., C) resembles the common eel in the elongated shape, in the absence of pelvic fins and in the narrow branchial openings, but it differs in the entire absence of the dorsal fin and the great elongation of the ventral which extends so far forward that the anus is under the head. The skin is scaleless. *Gymnotus* lives in the fresh waters of the Orinoco and Amazons and reaches a large size, the maximum being placed by some authorities at six feet, by others at eight. It lives only in swamps, or the shallow and stagnant parts of the river-systems. There are two electric organs on each side forming nearly the whole substance of the tail, if we include in that term all the part of the body behind the anus, that is to say almost four-fifths of the length of the fish; the upper organ is large, while the lower is quite slender and runs along the base of the ventral fin.

In the Mormyridæ, a family belonging to the primitive sub-

*CERATODUS AUSTRALIS*, THE AUSTRALIAN LUNG-FISH  
AFTER RASHFORD DEAN, FROM A SPECIMEN LIVING IN THE ZOOLOGICAL GARDENS



*SACCOBRYCHUS FOSSILIS*



THE ELECTRIC EEL, *Gymnotus electricus*



order of Soft-finned Fishes (Malacopterygii) and living in the Nile, Congo, and other rivers of sub-tropical Africa, there are two electric organs situated, as in *Gymnotus*, on either side of the tail, but of much less power. These fishes have a curious appearance on account of the shape of the head, which though differing much in the various species, is always more or less unlike that of a typical fish. In many species the snout is much elongated and bent in various ways, so that some resemblance to different mammals and birds is produced; thus one species suggests an elephant, another a horse, another a sheep, another a plover, another an ibis, etc. The mouth is always small, and in the species in which the snout is most elongated is reduced to a very minute aperture. In accordance with this the food consists of minute animals such as insect-larvæ and fresh-water crustacea, fragments of leaves and other vegetable matter. Professor Fritsch, who investigated the electric organs of these fishes in Egypt, states that they are, in contrast to other electric fishes, very active and excitable, and he found it very difficult to keep them alive in captivity. The electric powers of these fishes are very weak, and were formerly denied altogether; they seem to be of use only as a protection of the fish against enemies.

The last of the electric fishes<sup>1</sup> is the electric cat-fish *Malopterurus electricus*, one of the Siluridæ and therefore belonging, like *Gymnotus*, to the sub-order Ostariophysi. It is a curious fact that whereas in Torpedinidæ and Mormyridæ the electric organs are characteristic of the whole family they are confined in *Gymnotus* to a single genus and in *Malopterurus* to a single species. The electric cat-fish is also an inhabitant of Africa, occurring in all the large rivers of the tropical parts of that continent and extending to the lower Nile; it grows to a length of 3 ft. It is sluggish in its movements and lurks in dark places. Its flesh is used as food.

In structure the electric organs of all these fishes, with the exception of *Malopterurus*, are closely similar. Each organ consists of a number of columns of somewhat gelatinous tissue, lying parallel to one another and side by side, the surfaces in contact being somewhat flattened. These columns are separated by fibrous tissue, they run vertically in *Torpedo*, longitudinally in the other cases. Each column consists of a number

<sup>1</sup> See note, page 440.

of flat plates lying one over the other, and separated by partitions of fibrous tissue. Thus the organ is divided by the fibrous tissue into a number of flat compartments, and each compartment contains an electric plate. The latter is a muscular fibre, which has undergone a transformation, and consists of a special granular substance containing numerous nuclei, while on one side of it is a network of nerve-fibrils connected with one of the nerve-fibres derived from the nerves supplying the organ. In *Torpedo* the nervous expansion, which corresponds to the plate forming the nerve-termination on a muscle-fibre, is on the lower or ventral side of the electric plate, in *Gymnotus* it is on the posterior side. In each case the nervous side of the electric plate is negative to the other side, and the current of electricity outside the fish passes from the positive end of the organ to the negative. In *Torpedo* and various species of Skate the actual development of the electric plates has been traced out in the embryo, or young stages of the fish, and in the latter the characters of the modified fibres are not entirely lost in the fully developed organ. In the Skate it is seen that the muscle-fibres are flattened to form the plates from end to end, not sideways, and in fact in many cases the flattening is confined to one end of the fibre, that to which the nerve-ending is attached, while the other end is still elongated. In *Torpedo* the transformation of the fibres begins while they are still in a very embryonic condition, and proceeds so far that the adult structure bears no resemblance to muscle-fibres. There can be no doubt that in *Mormyrus* and *Gymnotus*, the electric plates are developed in the same way, though their condition in the embryo or young fish has not been investigated. It is not always possible to decide which particular muscles have been transformed into electric organs, but in *Torpedo* it is known that the organs are derived from the muscles of the outer parts of the branchial arches, and in accordance with this fact the nerves which supply the organs are branches of the cranial nerves. There are four of these nerves, of which the first is a branch of the fifth cranial nerve, the others, branches of the vagus. These nerves are enormously enlarged, and proceed from a special outgrowth of the brain, called the electric lobe, situated on each side, immediately below the cerebellum. In *Gymnotus* and *Mormyrus* the electric organs are derived from

parts of the lateral tail-muscles, and the electric nerves are branches of the spinal nerves.

The electric organs of the electric cat-fish, *Malopterurus*, differ in many characteristics from those of the other electric fishes. In this fish the organ consists of an almost uniform layer of gelatinous tissue situated beneath the skin and extending all round the body, from the level of the bases of the pectoral fins to the commencement of the dorsal adipose fin and the ventral fin which is opposite to the dorsal. The electric layers of the two sides are separated only by thin dorsal and ventral partitions of fibrous tissue. The tissue beneath the electric layer is continued behind into the ordinary tissue of the skin so that the electric tissue seems to be derived not from muscular tissue but from the skin. The organ in this case is not divided into columns of plates as in the other cases, but at the same time it consists of electric plates which are placed transversely to the length of the body. These plates are much smaller than those of the usual type of organ and are irregularly arranged; each one is flat and thin, circular in outline, and at the centre of each is a funnel-shaped depression projecting backwards, to the posterior end of which is attached the nerve-fibre. The plates, as in other cases, contain numerous nuclei and in minute structure are similar to the plates in the other cases. The electric condition of the plates is, however, just the opposite to that in other electric fishes, for the posterior face to which the nerve is connected is positive and the anterior face is negative; the posterior end of the fish is therefore positive and the anterior end negative, and the current of discharge passes from the tail to the head outside the fish. Still more extraordinary is the innervation of the organ in *Malopterurus*: on each side of the body the organ is supplied by a single large nerve-fibre, not a single nerve but a single fibre, which branches repeatedly, each ultimate branch being connected with a single plate as above described. Each of these two fibres arises from a single giant ganglion cell near the anterior end of the spinal cord, and the fibre emerges from the spinal canal by the first intervertebral aperture. The development of these organs is still unknown, even the smallest specimens of the fish hitherto obtained, only a few inches long, having the organs already developed and giving shocks like a succession of pricks when

held in the hand. It has been supposed that the plates in this case are developed from club-shaped cells like those seen in the epidermis but there is no proof of this, and one investigator thinks it is still possible that the organ in this case as in others is derived from muscular tissue.

There are two questions concerning the electric organs of fishes on which we have still to confess almost complete ignorance, firstly how the electricity is produced, secondly how the evolution of these organs is to be explained. With regard to the first we know that the passage of a stimulus along a nerve and a contraction in a muscle are accompanied by electric phenomena, in other words the normal functions of nerve and muscle produce electricity. When either nerve or muscle is at rest no electric current is produced, but when a stimulus passes along the nerve or a contraction along the muscle, the part of the nerve affected by the stimulus, or the part of the muscle which is contracting, becomes electrically negative to the parts at rest and if the negative part is joined by a wire to any other part a current passes along the wire. In the electric organ we have the electric plate derived from a muscle-fibre and the termination of a nerve-fibre on one side of it. The electric plate however does not contract and we do not know in what way it takes part in the production of electricity. If we suppose that the side where the nerve terminates becomes negative because it is strongly stimulated, while the opposite side remains unstimulated and is therefore positive, we have some idea how the electric organ is able to give electric shocks. From the fact that the nerves to the organs are so enormously developed and the fact that the tissue of the organ, originally muscular, has lost its power of contraction, we may conclude that the nervous part of the organ plays the chief part in the production of electricity. When two points some distance apart on the organ are joined by a conducting body one point will be negative to the other and a sudden discharge, that is a momentary current of very high voltage passes through the conducting body and has the same effect on other animals as an electric shock produced in any other way. The power of the *Gymnotus* is so great that when travellers cross a ford over a river where these fish are abundant their beasts of burden are frequently thrown to the ground as though struck by lightning.

In the case of the torpedo the shock sustained by a single person touching a healthy specimen at two points is strong enough to be very painful, and if a number of persons join hands and the person at each end touches the fish, a considerable shock passes through the whole series of persons. The electric condition to which the shock is due is apparently produced by nervous stimulation at the moment of the discharge, in consequence of the stimulation of the sensory nerves of the fish: anything touching the skin of the fish causes by reflex action stimulation of the electric nerves and so produces a shock, just as in ordinary cases a sensation of touch, that is stimulation of the sensory nerves of the skin, gives rise to a muscular contraction; and just as muscles and nerves become exhausted by muscular contractions, so the electric organs and their nerves become exhausted by discharges and only recover their power after a period of rest.

With regard to the evolution of electric organs, Darwin himself was much impressed by the difficulty of explaining their origin on his theory of natural selection. The difficulty is not so much the transitional stages from muscle to electric organs, since in the skates we have in existence all stages of the transition, but to understand how the rudimentary stages could be or have been of any use to the possessor, and therefore of what is called selection value. We can understand that a well-developed electric organ is of great use to its possessor either to paralyse its enemies or its prey, but we have no evidence that the slight powers of the organs in skates are of any use to those fish, since for some time electricians were unable to obtain any effects from them on electric apparatus. Even in the *Mormyridæ* the earlier experimenters were unable to obtain any electric effects from the organs. The theory of natural selection then affords no explanation of the evolution of these organs, as the accumulation of slight variations in the earlier stages seems impossible. On the other hand, we cannot at present point to any conditions of life which would produce directly the transformation of muscular tissue into electrical organs. We can only ponder over the apparent paradox that the increased stimulation and development of nerves that were originally motor should have been accompanied by the degeneration of the contractile property of the muscular tissue, considering that stimulation of such nerves

in other cases leads to the increased development of the muscles and their powers of contraction. It would seem that there is under certain circumstances a special kind of nerve-impulse which is specifically electric and produces electric changes instead of contraction. If this were the case the constant repetition of such stimuli might tend to produce the modification of muscular tissue which has taken place in the electric organs of fishes.

We have considered in the above pages some of the most striking facts concerning the life and structure of fishes, and may add a few general reflections suggested by these facts. It will be seen that while the truth of the general principle of evolution, the mere proposition that fishes like other animals have descended from remote ancestors through innumerable generations with various changes of structure, and wide divergences from the original type, is supported by the evidence of fossil remains, comparative anatomy, distribution and development, yet in seeking the explanation of this evolution in particular cases we are met with all sorts of difficulties. There may be some who think that Darwin's explanation, variation and selection, is sufficient, but there are others who insist on going farther and inquiring what are the causes of the variation and selection. If by selection is meant the advantage of every detail of structure in relation to a particular mode of life, it is impossible at the present day to uphold this view with regard to many of the most important characters by which fish are classified. We may conclude that the air-bladder arose as an advantage in muddy and fresh waters, and perhaps the gill-cover might be useful in these conditions though it is difficult to see how, but no valid reason has been given for the substitution of a bony skeleton, internal and external, for the cartilaginous skeleton and dermal denticles of the primitive shark-type. No satisfactory explanation in terms of utility has been given for the various steps of the transition from the Fringe-finned Ganoid to the ordinary Teleostean, or from the Soft-finned Fishes to the Spiny-finned, or from the shark-type to the Chimaeroid. Yet these are the principal differences by which fish are classified. Again, when we compare closely allied species with one another it is impossible to prove that the differences are differences of adaptation. In most

fishes adaptations exist, but they do not follow, in the majority of instances, the lines of classification: in some instances, *e.g.*, Skates and Flat-fishes they do, but these are rather the exceptions than the rule. It may be suggested that the apparently useless or indifferent characters are correlated with the useful, but of this there is no sufficient evidence. Again, it might be suggested that the distinguishing characters are or were originally the direct result of conditions, but we have no proof of this: we cannot say that fresh water produces bone, seeing that many of the most bony forms now exist in the sea. We are driven then to substitute for the terms variation and selection, the terms spontaneous variation and survival: we know that the new types which have arisen have survived and multiplied, but we have no right to assert that the distinguishing characters have been directly necessary or useful in the struggle for existence.

With regard to adaptations the question is different: here, admitting the advantage, we may doubt whether the variations were spontaneous, that is to say, independent of the conditions of life. If, for example, the bladder arose as a spontaneous variation we may ask how it is that it arose only when the fish was compelled to breathe air, why has no sign of it ever appeared in the shark type in the sea. Why is it that various adaptations for atmospheric respiration have arisen in different groups of fishes which were compelled to breathe air? Why is it that in the same fish in the individual lifetime the structure changes gradually when the habits change, as in the flat-fishes? It is true that to some extent the cartilaginous skeleton succeeds the notochord and the bone succeeds the cartilage, in individual development, but these changes do not correspond to changes of habit. In some cases we see similarity of habits producing similarity of form in fishes belonging to different groups, as in the numerous eel-like fishes which hide themselves in holes or burrow in the mud, for example cyclostomes, lung-fishes, electric eels, true eels, and blennies, fishes far apart in classification, and we cannot perceive that the fundamental differences between these types were all originally due to differences of habit. Enough has been said to show that the various theories of evolution are far from affording a satisfactory explanation of all the problems arising in the

study of fishes as of other animals, that the complicated phenomena are not to be explained by any one cut-and-dried formula. On the whole it seems most reasonable at present to conclude that the structure and evolution of fishes are due to the constant interaction of two general causes or processes, spontaneous variation or the occurrence of "mutations," on the one hand and the influence of the conditions of life on the other. The struggle for existence drives fishes, as other animals, to adopt various habits in order to obtain food, to escape enemies, and to produce offspring; the actions involved in these habits by "functional stimulation" produce changes of structure, and the results of these changes are adaptations, while at the same time the direct action of the conditions may produce results such as blindness in cave-fishes, and absence of pigment on the lower sides of flat-fishes. On the other hand, the differences which distinguish species, and the larger differences which distinguish the subdivisions of the class from each other, appear to be due in the great majority of cases to spontaneous variations or mutations which have no direct relation that we can perceive either to utility or adaptation, or to the habits or conditions of life.

NOTE.—In connection with the account of electric organs in fishes mention should be made of *Astroscopus y graecum* which occurs on the east coast of the United States of America. The organ in this fish is small and situated behind the eye on each side: it seems to be formed by modification of part of the eye muscles.

## SECTION IV

# CYCLOSTOMATA OR MARSIPOBRANCHS

### CHAPTER I

#### INTRODUCTORY

General structural characters and definition.

THE Cyclostomes or "Round-Mouths," including hags (Myxinoids) and lampreys (Petromyzonts), form a primitive class of vertebrates. They differ from fishes, (1) in having round suctorial mouths, without definitely developed jaws, (2) in the absence of paired fins, (3) in the peculiar purse-like gill-pouches, and (4) in showing many unique features such as the unpaired nasal sac. As the distinction between animals without jaws and animals with jaws is anatomically deep, the Cyclostomes stand apart from the Gnathostomes, which include fishes and all the other vertebrates. They represent a remnant of an ancient stock, and like other types which may be so described, *Amphioxus*, for instance, they show a combination of simplicity and specialisation. Their wide geographical representation may also be interpreted in relation to their ancient origin.

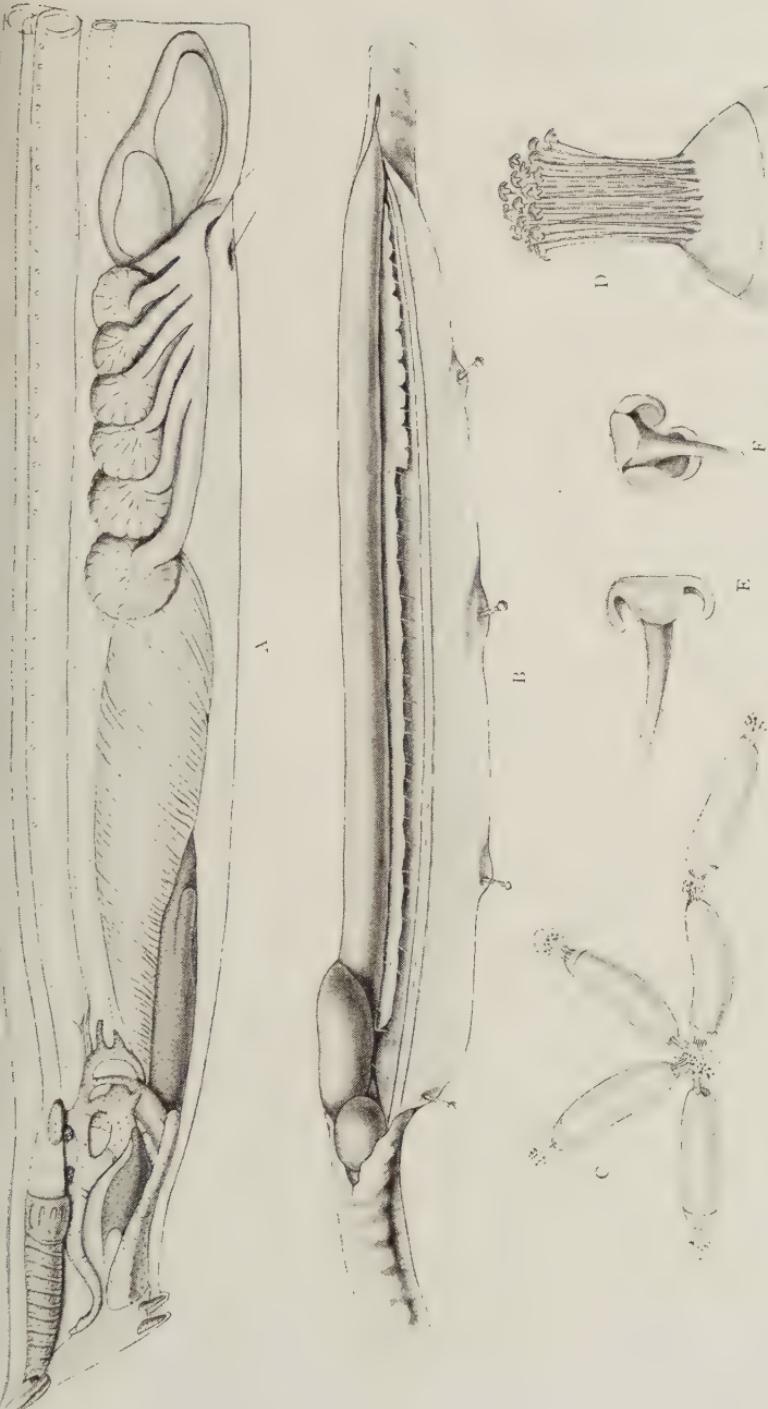
The Cyclostomes are marked by the following general characters: the eel-like form, the smooth scaleless skin; the absence of paired fins or girdles; the suctorial mouth, with horny teeth, without definitely developed jaws; the cartilaginous skeleton and persistent unsegmented notochord; the absence of dermal fin-rays in the unpaired fins; the single nasal organ curiously combined with the pituitary sac; the purse-like gill-pouches; the straight intestine; the absence of genital ducts.

## CHAPTER II

### MYXINOIDS OR HAG-FISHES

Characters. Habits. Mode of feeding. Life-history. Variability. Adaptations in struggle for existence. Classification.

THE Hags or Myxinoids are the simplest Craniates, and have many remarkable peculiarities. The body is eel-like and there is a row of large mucous glands on each side. Above the jawless mouth there is an unpaired nostril or naso-pituitary opening which leads into the buccal cavity and is the channel by which the water passes in on its way to the gill-pouches. Beside the mouth and the "nostril" there are four pairs of short tentacles or barbules. There is a single horny tooth on the roof of the mouth and on the floor there are two pairs of comb-like tooth-plates which are worked by a powerful muscular piston or "tongue," the huge development of which has pushed the heart and gill-sacs unusually far back. The gill-sacs open directly into the pharynx, and directly or indirectly to the exterior. In *Bdellostoma* they open directly to the exterior, in *Myxine* each is provided with an efferent canal, and the canals of either side open together on the ventral surface. In *Paramyxine* there is an interesting intermediate arrangement. There are only a few small cartilages corresponding to the lamprey's elaborate branchial basket. The brain is poorly developed, notably as regards cerebrum and cerebellum. The eyes are degenerate, without lens or muscles, and do not reach the surface. There is only one semicircular canal in connection with the ear, but it perhaps corresponds to two fused together. The Myxinoids are the only normally hermaphrodite vertebrates. The eggs are large and have horny shells with adhesive threads; as there is much yolk they divide partially. So far as is known the development is direct without larval metamorphosis. Myxinoids are widely represented in the seas of both hemispheres.



A. HAG-FISH (*MYXINE GLUTINOSA*) ANTERIOR END DISSECTED, TO SHOW THE SIX ROUNDED GILL-POUCHES, IN FRONT OF WHICH (TO THE LEFT IN FIGURE) IS THE TONGUE, MUSCLE, BEHIND, THE HEART. (AFTER W. K. PARKER)  
 B.-HAG-FISH OPENED TO SHOW HERMAPHRODITE GENERATIVE ORGAN IN THE MALE CONDITION. THE GENERATIVE ORGAN IS THE NARROW BAND JUST BELOW THE INTESTINE, AND THE POSTERIOR THIRD, WHICH IS SWOLLEN, IS THE MALE PORTION. C.—EGGS OF CALIFORNIAN HAG-FISH CONNECTED BY THEIR POLAR FILAMENTS. D.—POLAR FILAMENTS OF SAME ENLARGED. E, F.—ENDS OF SINGLE FILAMENTS MORE ENLARGED



A very valuable contribution to our knowledge of the habits of Myxinoids was made by Julia Worthington ("Contribution to our Knowledge of the Myxinoids," *American Naturalist*, xxxix., 1905, pp. 625-663) who had the good fortune to obtain several hundred individuals of *Bdellostoma dombeyi* Lac. of the Pacific Coast, and to succeed in keeping them in good condition in an aquarium. Some of the results of four months' observation may be summarised; they afford a good illustration of the study of habits.

The Pacific hag, which abounds in the Bay of Monterey, is usually found at a depth of about 50 fathoms, particularly on the rock-cod beds. In the aquarium, they preferred a hard bottom, and were fond of lying coiled among the rocks. "When well and at rest, the hag-fish is invariably coiled up more or less tightly, either in a spiral by itself, or in and out among the rocks. But if exhausted or sick, the coil straightens out, and it lies in a crescent form. The sicker it is, the straighter it becomes, and when dead it lies entirely straight." They are extremely sensitive to rise of temperature, though they are very hardy animals in most respects.

The habits of the European *Myxine glutinosa* are somewhat different. Mr. J. T. Cunningham in the years 1884-1886 kept numbers of specimens of this species in tanks with mud at the bottom, at Granton on the Firth of Forth near Edinburgh, and found that the animals always burrowed into the mud and remained quiescent in the daytime, with only the tip of the snout exposed. At this point is situated the naso-pituitary aperture, and the current of water entering this and escaping at the single pair of exhalent apertures further back could be clearly seen from the movement of particles of mud. As the *Myxine* were taken on muddy ground at a depth of about 40 fathoms, off St. Abb's Head, there can be no doubt that it is their natural habit to burrow into the mud. The difference of habit in the two cases probably corresponds to the difference in the exhalent gill-apertures, between *Myxine* and *Bdellostoma*, the former having a single aperture on each side, the latter a separate aperture for each gill-pouch.

Hags swim swiftly, with a graceful serpentine motion, but they prefer a quiet life, especially during the day. The muscle segments or myotomes alternate as they do in lancelets.

Regarding the Pacific hag, Miss Worthington writes: "When the night lines are examined, one-third or more of the hooks hold hag-fish, and the fish on many of the others have been entirely eaten away, nothing but the skin and bones being left. The hag-fish has bored inside the skin and eaten all the soft parts, and is sometimes caught in the very act of wriggling away at the close of its meal when the fish is taken from the water.

"The hag does not really suck the captured fishes, but it presses against them and rasps off pieces of skin and muscle. If the fish is a large one, the hag makes a hole through the body-wall and goes inside. Several often work together and I have seen three or four inside one fish. In captivity they eat at long intervals and seem able to remain vigorous on a minimum of food. From the nature of their diet it seems likely that opportunities for meals are not frequent in natural conditions, and it is probable that the hags have become constitutionally adapted to do with little food. The males of the Californian hag are known to be fond of the eggs, which they swallow whole.

"On the ventral wall of the pharynx there is a paired tooth-plate-- which some regard as representing the lower jaw. Each half of this plate bears two rows of horny teeth pointing backwards. When the hag feeds, the tooth-plate is thrust out of the mouth, and its fore end is drawn down so that it takes a position almost perpendicular to the long axis of the body. The two halves are at the same time drawn apart, so as to present an almost flat surface. Placing this flat surface against the fish to be eaten, the hag draws the halves of the tooth-plate together, thus tearing off a portion of the food, and then withdraws it into its mouth. It swallows the food very rapidly, and immediately sticks out the tooth-plate for more."<sup>1</sup> The tooth-plate is worked by five muscles, three of which form a long substantial "club," which may be readily felt on a spirit specimen of a hag stretching back for a couple of inches behind the mouth. *Myxine* treats the long lines of the haddock fishermen off the mouth of the Firth of Forth in the same way, many taking the baited hooks into their stomachs, others attacking the hooked fish.

There is no doubt that hag are found inside fishes, but

<sup>1</sup> Julia Worthington, 1905.

these are generally fishes which have been caught on the hooks of a long line, and were probably bored into after they had been hooked. It has been generally thought that the hags could not fasten on to a free swimming fish, they have no sucker as the lamprey has, and the teeth are not suited for gripping.

In Japan, however, Bashford Dean found that a species of hag common there frequently made its way into a floating cage and attacked and killed the living fish or squid contained in it. Hags are thus almost certainly able to attack living, active fishes in nature, but they are not parasites because they do not live for any considerable time within the living fish, the latter being killed by their attack.

The eggs are sausage-shaped, yellow in colour and about an inch in length. At each pole are a number of thread-like processes of the horny envelope, ending in triangular knobs, and these threads become entangled together so that the eggs laid at one time are connected together in a sort of string or chain. Mr. J. T. Cunningham showed in 1885 that the envelope with its threads was formed entirely in the ovary, not in an oviduct as is the case of Dog-fishes, since oviducts are entirely absent. He also showed that *Myxine* was usually hermaphrodite, the posterior end of the generative organ being male, the anterior end female, but both parts are not ripe at the same time. The same is not the case, according to the observations of Professor Bashford Dean, in the Californian hag, *Bdellostoma stouti*. In that species, although the structure of the organ is similar, the male and female parts are developed in separate individuals. Very few of the eggs of the European *Myxine* have been obtained, in spite of persistent endeavours, but Professor Bashford Dean was successful in obtaining considerable numbers of the fertilised eggs of the Californian hag. They were brought up by Chinese fishermen entangled on the hooks of ling lines. Professor Bashford Dean has published a fairly complete account of the development of the embryo within the egg up to the time of hatching.

The newly hatched animal (about  $2\frac{1}{2}$  in. in length) has the same shape as the adult. There is a marked increase in girth when about 15 inches long, but this does not seem to be connected with sexual maturity. The growth, like the de-

velopment within the egg, is slow compared with that of many other vertebrates.

One of the many interesting points about Myxinoids is the variability exhibited by *Bdellostoma* as regards the number of gills. A short account of this will serve to show how the study of variations bears on the study of species. The Californian hag has usually eleven or twelve gill-slits; it was called *B. stouti*. The Chilian hag with ten, was called *B. dombeyi*. The Cape of Good Hope hag, with six or seven, was called *B. forsteri*. Ayers studied these three species and came to the conclusion that they were really variations within one species which is best called *B. dombeyi*. A Japanese form which Bashford Dean called *Homea okinoseana* has eight gills, thus filling the gap between the Cape form and the Chilian form.

Miss Julia Worthington, combining the records of Dr. Gilbert and Dr. Ayers with her own, gives the following striking table:—

No. of Individuals.	No. of Gills.	Per Cent.
4	10-11	·41
236	11	24·63
95	11-12	9·92
574	12	59·52
33	12-13	3·44
16	13	1·67
—		
958		

Twelve on each side is the number *most commonly found* in the Californian hag, but as it only occurs in about 60 per cent in a total of 958, it may be said that eleven and twelve are the usual numbers. It is very striking to find that 13·7 per cent (out of 958) have more gills on one side than on the other. In this connection Miss Worthington observes: "With six and seven gills the prevailing number in *Bdellostoma forsteri*, eight in that found in Japan, ten the number in the Chilian form, and eleven and twelve in California, varying on the one hand, though rarely, to ten, and on the other hand, more frequently, to thirteen, it is surely no longer possible to divide these animals into different genera and species on the basis of the number of gills alone; the count of teeth (Ayers, 1894), is equally unsatisfactory as a ground for division into species, and no other ground for such division has ever been advanced." It should

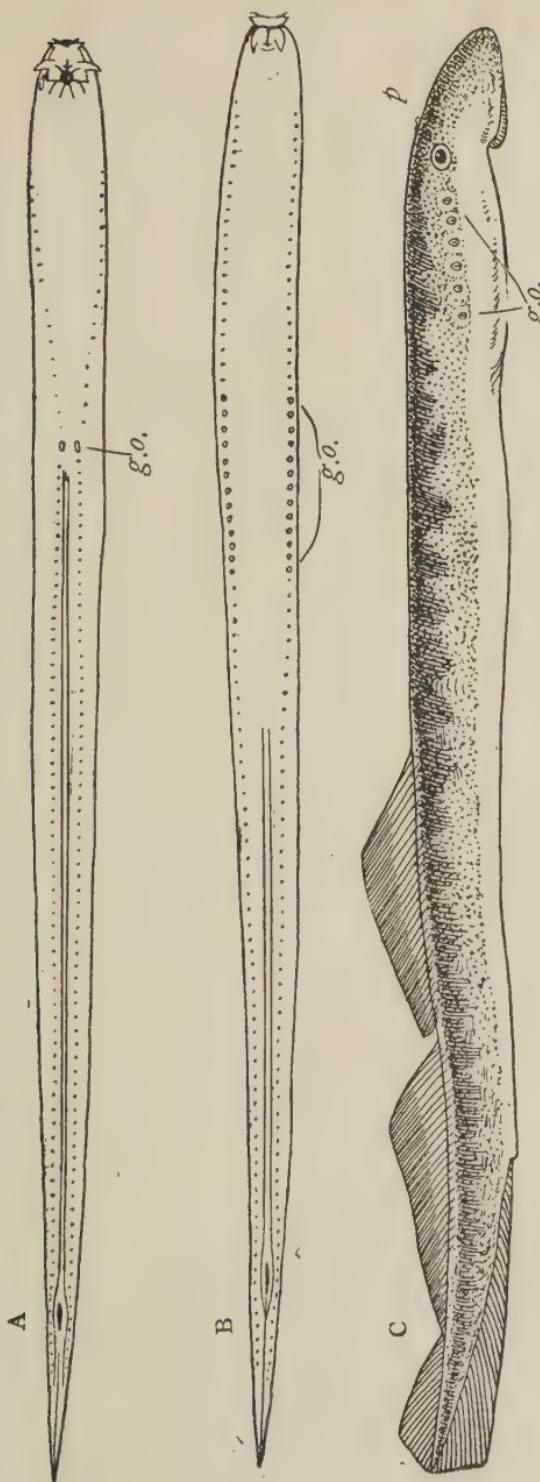


FIG. 32—A, The Hag-fish, *Myxine glutinosa*. B, Californian Hag-fish, *Bdellostoma stotii*. C, River Lamprey, *Petromyzon fluviatilis*. A and B, From ventral surface. C, From side. *g.o.*, Gill-apertures, one pair in A, thirteen pairs in B, seven pairs in C. *p*, Pituitary opening.

be noted perhaps that the variability is really much greater than is indicated, for there are many variations in anatomical detail apart from numbers.

There is no doubt that the slime so abundantly secreted is protective. It flows out copiously in viscid threads when the hag is excited, and it forms a slippery sheath which makes it difficult for one to grip the animal.

#### DIFFERENT KINDS OF MYXINOID

*Myxine*.—In the genus *Myxine* there are not more than six pairs of gill-sacs, which have a common external aperture on each side. The genus is represented in the Atlantic, the North Sea, and the Pacific. The North Sea species is *Myxine glutinosa*, which may attain a length of nearly 2 ft. The North American form is sometimes distinguished as *M. limosa*.

*Paramyxine*.—In the genus *Paramyxine*, from the Pacific, the connection of the gill-sacs with the exterior is intermediate between that in *Myxine* and that in *Bdellostoma*.

*Bdellostoma*.—In the genus *Bdellostoma* from the Pacific e.g., off California and Chili, there are six to fourteen pair of gill-sacs, all opening separately. The common Californian species, which has been most studied, is *B. dombeyi*.

## CHAPTER III

### PETROMYZONTS OR LAMPREYS

Characters. Habits. Mode of feeding. Life-history. Classification. Relationships of Cyclostomes.

THE lampreys are marked by many interesting peculiarities, which show that they are not *nearly* related to the hags. The mouth is surrounded by a large succatorial funnel, which is studded internally with numerous horny "teeth". Other similar teeth are borne on the muscular piston or "tongue". In consequence of the great development of the sucker, the nostril or naso-pituitary aperture is far back on the top of the head. The canal does not, however, open internally on the roof of the mouth as it does in the hag. There are seven pairs of gill-sacs which open directly to the exterior, and, in the adult, indirectly into the gullet. In the larva the gill-sacs open, as usual, into the pharynx, but at the metamorphosis the part of the gut which receives them is converted into a suboesophageal respiratory tube and a new anterior oesophagus is developed. There is an elaborate branchial basket supporting the gill-sacs, the "tongue," and even the heart. Lampreys have normal eyes; the ear has two (instead of the usual three) semicircular canals; there is a well-developed lateral line system of sensory structures (of which there is just a trace in the head region of the Californian hag); the dorsal and ventral roots of the spinal nerves do not unite; the brain is poorly developed. There is a *fairly* well-developed cartilaginous skull. In the intestine there is a hint of the spiral fold, which is large in gristly fishes, serving to increase the digestive absorptive surface. The eggs are small and thin-shelled. As there is relatively little yolk, the segmentation is total. The embryo develops into a larva which is in many respects different from the adult. There is a marked metamorphosis. Lampreys are

represented both in the rivers and the seas of Europe, Asia, North and South America, and Australia.

There is no doubt as to the exclusively marine character of Myxinoids, but the case of the lampreys is more difficult. As all of them, so far as we know, ascend rivers for spawning, and as the environment of the young is usually indicative of the original home of the parents, it is likely that the lampreys represent a fresh-water Cyclostome stock. It may be recalled that the salmon, first cousin to the trout, and essentially a fresh-water fish, spawns in the rivers, though it does most of its feeding and growing in the sea. On the other hand, the common eel is essentially a deep-water marine fish and spawns in the great abysses, though it does most of its feeding and growing in the fresh waters. Although various authorities state with some emphasis that most lampreys are marine, it is more probable that the Petromyzonts represent a section of the old Cyclostome race that took upon itself the problem of trying the fresh waters for what they were worth. This may serve to illustrate the zigzagness of pedigrees. The main stock of Chordates was undoubtedly marine; the lampreys, primarily adapted to the "Sturm und Drang" of littoral life, went upstream; a large number became fresh-water animals. They visit the sea, like the salmon, to feed and grow lusty; they visit the fresh water to spawn and die!

Lampreys are carnivorous, and most of them are in the habit of fixing themselves to the bodies of fishes by means of their suctorial mouth-funnel, rasping off scales and skin and muscle with their teeth, and then sucking in the blood and pieces of loosened flesh. They take a very firm hold of their victims, and are difficult to dislodge. Experiments by Miss Dawson (*Biological Bulletin*, ix., 1905, pp. 1-21, 91-111) show that the funnel of a dead brook-lamprey (*Lampetra wilderi*) becomes firmly attached to a perfectly smooth surface when pressed against it with the fingers; how much more firmly will the muscular funnel of the living animal adhere. It seems, too, from Miss Dawson's experiments that a lamprey can shift its hold of the fish without actually loosening it. They most frequently attach themselves on the side under the pectoral fin, and "their hold is probably seldom loosened by any fish except by accident". "The relentless

voracity of these fearful pests of our fresh waters is shown by the deep holes<sup>1</sup> which they make in the living bodies of their victims, and by their own intestines gorged with blood and flesh" (S. A. Forbes and R. E. Richardson, *Fishes of Illinois*, 1908, p. 6).

It is doubtful whether adult lampreys eat anything but fish though it is often said that they take worms, insects, and decaying animal matter. Some small creatures may come in from the perforated intestines of the fishes that have been destroyed.

Most attention has been paid to the breeding habits of the brook-lampreys—*Lampetra planeri* in Europe and *Lampetra wilderi* in North America, "The females spawn in shallow water, and, as a rule, where there is some current over pebbly or stony bottom near the headwaters of a stream. During the spawning process the females cling with their oval mouths to pebbles or stones, with the body streaming in the current, and are clasped at the nape by the suctorial disks of the males" (Forbes and Richardson, *Fishes of Illinois*, 1908).

There is a lack of precise information in regard to the reproduction of lampreys. It is known that the reproduction is associated with profound constitutional changes in the body of both sexes, and that death often follows the spawning season. Large marine lampreys are sometimes found lying dead in the water just after the spawning—a signal instance of the nemesis that often follows reproduction. We know that many insects such as may-flies, and many butterflies die after reproducing, and the same is true of simpler organisms like many worms, and of higher organisms like the common eels. Reproduction is often the beginning of the end of the individual life; in the case of the lamprey (in some species at least) death follows rapidly on the heels of the generative process. In regard to the small American brook-lamprey (*Lampetra wilderi*) "spawning and death are said to follow so soon after the transformation that the parasitic stage appears to be quite passed over in the life-cycle, the adults not taking food of any kind" (Forbes and Richardson, *Fishes of Illinois*, 1908).

The newly hatched young lamprey is spoken of as a *larva*,

<sup>1</sup> For photographs showing the work of lampreys see H. A. Surface, *Bull. U. S. Fish Commission*, 1898, pp. 209-215; and 4th Ann. Report Fish, etc., New York, 1898, pp. 191-245.

because it is in many ways different from the adult, and does not become like the adult until it undergoes a metamorphosis. For a long time it was supposed to be a distinct animal both by zoologists and country people, the former calling it *Ammonoctetes* and the latter a "niner". A Strasburg fisherman called Baldner, seems to have convinced himself more than 200 years ago that "niners" grew into lampreys, but his correct conclusion was not generally accepted till long afterwards. Among the differences between larval and adult form, we may note that the eyes of the larva are far below the surface, that the mouth of the larva is horse-shoe-shaped rather than circular, and that the larva has no teeth. The upper lip of the larva is somewhat hood-like and the much shorter lower lip is included within it. Niners remain niners for three to five years, and the change to the adult form takes seven or eight months in the case of the brook-lampreys (September to April).

When the larva is hatched it burrows into the mud, where it lives on microscopic organisms wafted into the mouth by ciliary action. It is for some time sightless, the eyes being far below the surface. Both these points are of evolutionary interest: the abundance of cilia in the front part of the alimentary tract is a primitive feature, recalling the state of affairs in the lancelets; and the position of the eye reminds us that the eye of Vertebrates is a "brain-eye," i.e. that it grows from within outwards, whereas the eyes of Invertebrates are skin-eyes arising on the surface. As the brain is developed from an insinking of superficial ectoderm cells, the contrast between brain-eye and skin-eye is not so sharp as at first sight appears. It may also be noted that the eye of the hag remains hidden throughout life; it never reaches the surface at all.

The larva lives a rather sluggish life wallowing in the mud, especially in slow-flowing reaches or backwaters of the river. Alcock<sup>1</sup> has discovered the interesting fact that the skin secretes a digestive ferment which protects it from the injurious action of Bacteria and Fungi.

#### DIFFERENT KINDS OF LAMPREYS

*Petromyzon*.—For the most part northern forms, such as *Petromyzon marinus*, about a yard long, which spawns and

<sup>1</sup> *Journ. Anat. Physiol.*, xiii., pp. 612-637.

spends its larval life in fresh water. This large lamprey is found along the coasts of Europe and North America, and is represented in the interior waters of New York by a land-locked variety.

*Ichthyomyzon*.—Girard. Small lampreys, confined to the rivers of the Mississippi Valley and eastern United States. The supraoral plate is typically armed with two or three (sometimes four) separate teeth, set close together; the anterior lingual tooth has a median groove; the dorsal fin is continuous with a broad and shallow notch. Example: *I. concolor* (Kirtland), the silvery lamprey, ten inches long.

*Lampetra*.—Small lampreys of the streams of Europe and North America. The supraoral plate is crescent-shaped, with a large bluntnish cusp at each end, separated by a very small median cusp; the lingual teeth are small, with dentate edges, the median denticle enlarged; the dorsal fin has a sharp notch or is entirely divided. Examples: *Lampetra planeri*, the lesser fresh-water lamprey of Europe, usually under a foot in length, and the North American *L. wilderi*, 6 to 10 in. in length, apparently not attaching itself to fishes.

Besides these genera there are others: e.g., *Mordacea* on the coasts of Chili, Australia, Tasmania; *Geotria* on the coasts of Chili, Australia, New Zealand.

#### AFFINITIES OF CYCLOSTOMES

(1) It must be admitted that Cyclostomes and fishes have several features in common besides the essential vertebrate characters. In both classes, for instance, there is a two-chambered heart which drives the blood by a ventral aorta to the gills.

(2) But if the word "fish" is to mean anything precise, it cannot include Cyclostomes, if only because they are jawless.

(3) That they are not degenerate fishes, is plain when we consider, for instance, the muscular rasping "tongue," the peculiar naso-pituitary canal, and the saccular gills.

(4) That the Cyclostomes probably diverged from the vertebrate stem at a level far below that of fishes, is suggested by many facts, such as the absence of jaws, the persistent unsegmented notochord which is continuous in front with the

posterior part of the skull, the less specialised head muscles, the lowly organised brain, the primitive nature of the excretory system, and the absence of genital ducts.

(5) It is probable enough that although the Cyclostomes are not degenerate fishes, they may be in certain respects degenerate, *e.g.*, as regards the eye in Myxinoids or the liver in the lamprey.

(6) "In the Ammocoete many remarkable features bridge over the gulf between the Craniata and the Cephalochorda. The mouth is bounded by lips; there is neither sucker nor horny armature, nor yet any rasping "tongue". The buccal cavity is separated by a velum from the pharynx, and this is limited in front by an encircling ciliated groove (like that of *Amphioxus*) which is at the level formerly occupied by the transitory first gill-slit. The groove is carried back along the floor of the pharynx into the opening of the thyroid gland. This gland develops as a mid-ventral outgrowth of the pharynx, acquires a lumen of considerable size, and along its folded walls become differentiated four rows of mucous cells. In fact, the whole structure bears a striking and unmistakable resemblance to the endostyle of the Tunicata and Cephalochorda, with which it is no doubt homologous" (E. S. Goodrich in Part IX. of Sir Ray Lankester's *Treatise on Zoology*, 1909, p. 52).

(7) From the Middle Old Red Sandstone of Caithness, Dr. R. H. Traquair described a minute extinct fish-like creature which he suggested might be a Cyclostome. It is a dainty little creature, somewhat tadpole-like at first sight, usually under an inch in length. The following characters point to affinity with Cyclostomes:—

- (1) "The skull is apparently formed of calcified cartilage, and devoid of discrete ossifications."
- (2) "There is a median opening or ring, surrounded with cirri, and presumably nasal, in front of the head."
- (3) "There are neither jaws nor limbs."
- (4) "The caudal fin is supported by median prolongations of the neural and hæmal arches, forming rays, occasionally forked, very like those of the lamprey."

But the vertebral column has numerous ring-like centra which is very unlike the state of affairs in Cyclostomes, and

there are other serious difficulties against ranking *Palaeospondylus* with the Cyclostomes.

(8) We cannot venture to say anything regarding the position of a very puzzling set of extinct animals (Silurian and Devonian) known as Ostracoderms or Hypostomata, but perhaps they should be mentioned here. They were without jaws, without a segmented axial skeleton in the trunk, without any trace of girdles, and they had a complex dermal armature, with a head shield. Examples: *Pteraspis* and *Cephalaspis*, both without paired limbs; and *Pterichthys* and *Bothriolepis*, with strange armoured appendages fixed to the antero-lateral angles of the body-shield.



## SECTION V

# THE LANCELETS— CEPHALOCHORDA

General position. External appearance. General characters. Functions and habits. Development and life-history. Relationships. Classification. Distribution. Features of special evolutionary interest.

NEAR the base of the great series or phylum of back-boned animals (*Vertebrata*) a place must be found for a number of small semi-transparent widely distributed marine animals known as lancelets. One of the best known is called *Amphioxus lanceolatus* or *Branchiostoma lanceolatum*. It is a matter of opinion whether they should be included within the *Vertebrata*, or kept by themselves in the vicinity of *Vertebrata*, and grouped along with Tunicates and acknowledged *Vertebrata* under the general heading *Chordata*. We shall return to this question; in the meantime it is enough to say that the Lancelets are either simple *Vertebrates*, or are allied to simple *Vertebrates* and at a somewhat lower grade. Their chief interest for the zoologist is their threefold simplicity. (a) There is simplicity in some parts of their organisation—but this is combined with a remarkable complexity in other parts; (b) there is, in certain respects, an interesting simplicity of function, e.g., as regards digestive system, sensory system, circulatory system. But again it will be seen that the physiology of the whole pharyngeal region is much more complex than in higher animals; (c) thirdly, there is simplicity in many respects as regards the development. Several considerations lead one to think that the Lancelets are much less primitive than they at first sight appear. They are probably derivatives of a primitive stock which have specialised on a line of their own—a *cul de sac* as regards higher forms.

*External Appearance.*—Lancelets are semi-transparent, often slightly iridescent animals, pointed at both ends, two or three inches long, with the body slightly flattened from side to side. The living animals are much plumper than those which have been preserved in spirit would suggest. All along the body there are V-shaped markings, with the apex of the V directed forwards ; these are due to cross-partitions of connective tissue that divide the longitudinal muscles of the sides of the body into *segments* or successive blocks. An interesting detail is that the segments of the two sides are alternate, not opposite. Thus the 27th block (or myotome) on the left is opposite the 26th partition (or myocomma) on the right.

The mouth is just behind the anterior tip of the body and is surrounded by delicate ciliated processes, called cirri, which waft in food particles. The anus opens ventrally on the left side not far from the posterior end. A ventral groove extends from the mouth backwards for about two-thirds of the length of the body, and is bounded by hollow side folds (metapleural folds), which converge at an opening called the atrial pore. A delicate fold of skin, supported by minute rodlets, runs along the middle line of the back, round the tail end, and along the ventral surface as far as the atriore.

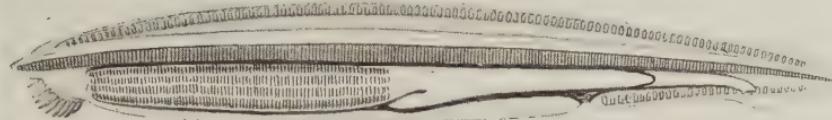
It is not the aim of this book to give an account of the detailed structure of types, and we do not propose to depart from this rule even in the case of the lancelets which stand so much by themselves. There are many admirable anatomical accounts (*e.g.*, those of Lankester, Sedgwick, and Herdman) and the annotated diagrams on Plate XXXIV. will give a clear picture of the general features—which is all that we require for our present purpose. Let us seek, however, to sum up these general features so as to make plain that the Lancelets are indeed very remarkable animals.

The Lancelets are chordate animals inasmuch as they possess (1) a dorsal tubular nerve-cord (without more than a hint of a brain); (2) a dorsal supporting axis (a persistent unsegmented notochord); and (3) a number of gill-slits, which open in the young animal from the pharynx to the exterior. In regard to each of these three points, however, there are remarkable peculiarities :—

- (1) The most anterior part of the nervous system is not



A



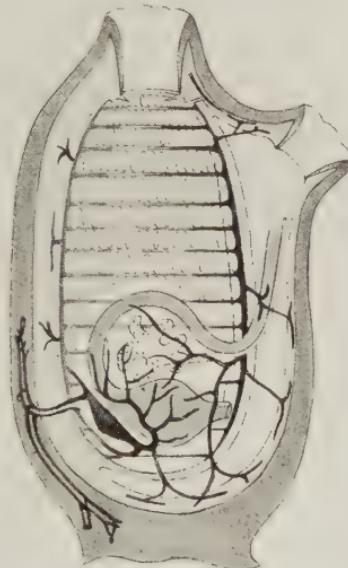
B



C



D



A. -AMPHIOXUS, EXTERNAL SURFACE LEFT SIDE: THE MOUTH SURROUNDED BY THE ORAL CIRRI IS ON THE LEFT. B. -AMPHIOXUS DISSECTED, SHOWING PERFORATED PHARYNX, AND BEHIND THIS THE STRAIGHT INTESTINE. ABOVE THE INTESTINE IS THE NOTOCHORD, AND ABOVE THIS THE NERVE-CORD. C. LARVA OF AMPHIOXUS ENLARGED, LYING ON LEFT SIDE, ON WHICH IS THE LARGE MOUTH: THE GILL OPENINGS TO THE RIGHT OF THE VENTRAL EDGE, BETWEEN THE TWO ATRIAL FOLDS. D. A SOLITARY ASCIDIAN (*ASCIDIA MENTULA*), LEFT SIDE EXTERNAL SURFACE. E.—THE SAME, INTERNAL STRUCTURE SHOWING PHARYNX INTESTINE, HEART AND BLOOD-VESSEL (IN BLACK)



the thickest. There is practically no brain, though the two pairs of nerves which pass to the sensitive front and above the mouth are different from the other nerves and may be called cerebral. There are many peculiarities in the spinal cord: thus there are two pairs of spinal nerves (instead of the normal one pair) for each myotome, there are no spinal ganglia or sympathetic ganglia. There is no brain-eye; what is sometimes called an "eye-spot" in front of the end of the nerve-cord being only a pigment spot. Another remarkable peculiarity is the occurrence of "spinal eyes" at regular intervals right down the nerve cord, beside and below the central canal. Each consists of two cells—a pigment cell and a percipient cell. They seem to be sensitive to light which passes through the translucent body.

(2) The notochord is a solid elastic rod with a thin sheath of connective tissue, but it is not even at the level of cartilage in the strict sense. It consists of vacuolated cells, and its supporting power is probably in great part due to their turgidity, as in many vegetable structures. Another quite unique peculiarity is that the notochord is prolonged beyond the end of the nerve-cord to the very tip of the body.

(3) The gill-slits are numerous, sixty pairs or so, while in fishes they do not exceed eight pairs. Moreover, the number is added to posteriorly during the *adult* life of the Lancelet. Primarily, the gill-slits open directly to the exterior, but they soon come to open into a special chamber—the atrial chamber—which communicates with the exterior by the atriore.

Thus we can define the Cephalochorda as follows.

There is a tubular nerve-cord along the dorsal or blastoporal surface, arising as an ectodermal median groove which becomes a canal. It shows in the embryo a temporary posterior connection with the gut-cavity called the neureneric canal. There is hardly any brain, though the first two pairs of nerves may be called cerebral. The dorsal and ventral roots of the spinal nerves do not unite. There are no brain-eyes nor auditory organs.

The notochord, which arises as an axial differentiation of cells along the median dorsal line of the primitive gut or archenteron, is persistent and unsegmented. It extends to the very anterior tip of the body, beyond the front of the nerve-

cord and, though skeletal, does not attain to the definiteness of cartilage.

The gill-slits on the pharynx become very numerous, and each is divided into two by a curious "tongue-bar"; in the adult they open not to the exterior, but into an ingrowing (ectodermic) atrial or peribranchial cavity, which obliterates most of the body-cavity or coelom in the pharyngeal region. The body-cavity arises as a set of pouches from the primitive gut (enterocoelic mode of origin).

The muscular system is very markedly segmented, the body-wall showing over fifty myotomes; the gonads are also segmentally disposed.

As regards the general scheme of the circulation there is a resemblance to that in fishes, but Lancelets are widely removed from fishes by the absence of vertebræ, limbs, skull, jaws, differentiated brain, sympathetic nervous system, brain-eye, ear, definite heart, pancreas, spleen, and genital ducts.

In certain respects, such as the persistently obvious segmentation of the whole body, the state of the nerve-cord and notochord, the numerous separate nephridia, and the segmental gonads without ducts, the Lancelets are primitive.

The eggs segment wholly, a typical gastrula is formed by invagination, the nervous system and the notochord arise in a very typical way, the mesoderm arises from mesodermic coelomic pouches.

The larval forms are strangely asymmetrical and the larval period is prolonged.

The following conclusions may be drawn concerning the relationships of Lancelets:—

I. There is no longer any doubt that *Amphioxus* belongs to the Chordate series.

It has (1) a dorsal, tubular, spinal cord, (2) a dorsal supporting axis or notochord, (3) pharyngeal gill-slits, and (4) a segmented body. We miss altogether the characteristic Chordate eyes (arising as paired outgrowths from the brain); we note also the absence of a definite heart (arising from the specialisation of part of a ventral blood-vessel or of two ventral blood-vessels), but there are numerous "hearts," as it were, taking the place of one, and the general course of the circulation is vertebrate-like; there is a total absence of elements

which are characteristic of all higher Chordates, viz., hair-cells responding to vibrations in fluid; and very noteworthy is the poor development of the brain, if indeed that term is permissible where there is little more than a slight enlargement of the anterior end of the nerve-cord. But when we admit all that, and admit also that *Amphioxus* shows some similarities to annelid worms, e.g., in its nephridia and in its eye-spots, it remains safe to say that the Lancelets are genuine Chordate animals.

We give a quotation from a paper by Prof. J. B. Johnston to illustrate the working-out of this argument in detail as regards the nervous system (Johnston, 1905, pp. 125-126).

"The nervous system of *Amphioxus* agrees with that of lower fishes in the following respects:—

- "(a) It is dorsal, hollow, and has separate dorsal and ventral roots of definite composition. The canal has an enlargement at the anterior end, the brain ventricle.
- "(b) The dorsal roots consist of general cutaneous, visceral sensory and visceral motor components. They contain also in the head region fibres of special sense-organs (olfactory or gustatory?)
- "(c) Both kinds of sensory fibres have ganglion cells which are situated either within the cord or in the root of the nerve in essentially the same position as the spinal ganglia of vertebrates.
- "(d) The two kinds of sensory fibres on entering the cord form dorsal tracts similar to those in vertebrates. Many cutaneous fibres show the bifurcation characteristic of these fibres in vertebrates.
- "(e) The viscero-motor cells are situated as in vertebrates dorsal to the somatic motor-cells, lateral to the ventral part of the canal.
- "(f) The nerve-cells retain the position and characters which are typical in the embryos of vertebrates and which are seen in certain parts of the brain of many fishes.
- "(g) The ventral roots arise separately and remain independent. They are true somatic motor-nerves."

II. Our second conclusion is that *Amphioxus* is a primitive

*Chordate type.* The nervous system is primitive in several ways, e.g., in the very slight development of the brain region, in the separateness of the dorsal and ventral roots, and in the somewhat embryonic position and character of the nerve-cells. There is also primitiveness in the persistent unsegmented notochord, the large number of gill-slits, the persistence of myotomes all over the body-wall, the numerous separate nephridia, the numerous segmentally arranged gonads. Compared with fishes, the Lancelets are primitive in their negative characters, namely, in the absence of limbs, skull, jaws, differentiated brain, sympathetic nervous system, cerebral eyes, ears, definite heart, pancreas, spleen, genital ducts. Even the mode of ingestion by the ciliary inwasting of particles is very primitive. All things considered, the most straightforward view seems that which regards this type as an offshoot from a primitive vertebrate stock. It is necessary, however, to consider an objection that is often raised: may not the apparent primitiveness have resulted from degeneration?

III. It is always possible to interpret comparatively simple types in two ways in their relation to less simple types belonging to the same series. On the one hand, we may suppose that the simpler types represent lower levels in the evolution of the series in question, or offshoots from these lower levels. Thus, it is usually supposed that Selachian fishes represent an older stock than Teleostean fishes—a lower branch of the piscine genealogical tree. On the other hand, we may suppose that the simpler types are the results of a process of degeneration from higher types. Thus, it is usually supposed that the typical Ascidiants have undergone degeneration. To take an illustration from another field, the winglessness of Collembola and Thysanura is doubtless primitive and so are many other features in these simple insects; but the winglessness of lice or of fleas is doubtless secondary, and the result of degeneration. Our immediate problem, then, is this: How far may the relative simplicity of *Amphioxus* be regarded as the result of a derivation of this type from some higher Chordate type?

When we consider the intricacy of certain structures in Lancelets, such as the oral vestibule, the pharynx, the atrial cavity, and the nephridia, we do not find any warrant for re-

garding Lancelets as derivable from higher Chordates. Nor does the development of Lancelets at all favour the idea that they are degenerate.

IV. There seems to be affinity—though not very close—between Lancelets and Tunicates. In both cases the walls of the pharynx are perforated by numerous gill-slits; in both there is a peribranchial cavity; in both there is an endostyle; there are several other resemblances all relating to remarkable structural features. On the other hand, the Ascidiants differ from the Lancelets in a great many ways—the presence of test, heart, and genital ducts; the absence of segments, of nephridia, and of any trace of coelom in the adult. The general habit of life is very different and the Ascidiants are hermaphrodite. The early stages in development in Tunicates and Lancelets have much in common, but after these are past there is great divergence. Now when we find very striking resemblances, e.g., in the pharynx, and very striking differences, e.g., as regards segmentation, we are led to the conclusion that Lancelets and Tunicates, though not nearly related, are descended from common ancestors, and that these ancestors diverged from the main Chordate stock, which led on to fishes and other Vertebrates.

#### CLASSIFICATION

There is not as yet unanimity in regard to the number of genera of Lancelets; we give Dr. Arthur Willey's version of what is always a difficult matter. Two genera may be distinguished, one including those species with paired reproductive organs, the other including those with unilateral reproductive organs. For the first the most correct title seems to be *Branchiostoma*, Costa, and it includes the sub-genera *Amphioxus*, *sensu stricto*, Yarrell, and *Dolichorhynchus*, Willey. For the second genus the name is *Heteropleuron*, Kirkaldy, and it includes as sub-genera *Paramphioxus*, Haeckel; *Epigonichthys*, Peters; and *Asymmetron*, Andrews.

An important general fact may be illustrated by the geographical distribution of Cephalochorda, namely, that old-fashioned types often have a very wide representation. We see this in some terrestrial types like *Peripatus* and its allies and in some fresh-water types like the Dipnoi or mud-fishes;

one of which occurs in Africa, another in South America, and a third in Australia. We may take the Cephalochorda as an illustration among marine animals. The meaning of the wide representation of archaic types is, in part at least, that having lived as a race for long ages they have had ample time and many opportunities for wide dispersal. The fact in regard to Lancelets is that they are found in relatively shallow water (rarely below 50 fathoms) in *all* temperate, tropical, and sub-tropical seas. Various species are reported from off the coasts of Europe, North America, South America, Queensland, Japan, Pacific Islands, Ceylon, Bahamas, etc.

Lancelets feed on microscopic particles and organisms which are swept into the mouth by the ciliated cirri. There is no evidence of seeking or selecting food. Along the ventral median line of the pharynx there is a glandular and ciliated gutter, similar to the endostyle of Tunicates, and this secretes mucus which is wafted forwards and entangles the food particles. Thin ropes of these pass backwards along a dorsal groove to the digestive portion of the food-canal. The gut is ciliated throughout, which is undoubtedly a primitive character.

Water is always passing in by the mouth, through the numerous slits in the pharynx into the atrial cavity, and out by the atrio pore. This current secures the aeration of the colourless blood in the delicate blood-vessels that run between the slits. Thus the current of water has both a respiratory and a nutritive significance just as in Tunicates. The current also serves to waft out the ova and spermatozoa, for there are no genital ducts. It is said that the current is sometimes reversed, which explains how the sex-cells, which usually escape by the atrio pore, occasionally pass out by the mouth.

The simple pouch or cæcum which projects forwards at the beginning of the digestive region of the gut is very interesting, since it remains permanently at a level which represents the early embryonic state of the liver in higher Chordates. No food is found in the cæcum ; it is a simple glandular diverticulum.

The excretory tubules or nephridia which filter the blood and get rid of nitrogenous waste products, are co-extensive with the gill-clefts ; they are situated in the body-cavity and open into the atrial cavity. There may be ninety pairs of these nephridia which in general disposition and in some de-

tails irresistibly take our thoughts back to those of Annelid worms. There is also what may be a vestige of an ancient excretory system in a pair of brown funnels, which extend between body cavity and atrial cavity, opposite the posterior end of the pharynx.

Lancelets are very muscular animals, the proportion of muscle to the rest of the body being unusually great. As we have noticed, the muscles are arranged in segments, a primitive condition seen in all vertebrate embryos, and visible throughout life in most fishes. The muscle-segments or myomeres are like widely open V's with the apices directed forwards. They are separated by partitions of connective tissue to which the numerous longitudinally disposed and flattened muscle-fibres (that compose each segment) are attached both in front and behind. In this, and in the dove-tailing, and in the fact that the muscle-segments of the two sides alternate, we see adaptations to energetic movement. The body is bent from side to side, as in fishes, the muscles of one side contracting while those of the opposite side are relaxed.

"The locomotion of *Amphioxus* is a rapid, curiously irregular wriggle, often accompanied by somersault-like movements" (Parker, 1908). It can swim head first or tail first. When the tail is stimulated, the animal moves head first; when the head or anterior region is stimulated, it moves tail first. Although its movements are energetic, they cannot be kept up for more than a few moments; the animal soon drops down and lies motionless, and it becomes unresponsive if it is excited repeatedly within a short time.

Lancelets are characteristically burrowing animals. When they drop on to the sandy bottom they may disappear with a sudden spring, or they may lie for a time straightened out, and then arching their bodies disappear beneath the surface. They often lie with the mouth agape protruding on the surface of the sand. They usually enter the sand tail foremost, but sometimes the head goes in first. While the free individuals are always straight, those buried may have "a very tortuous outline, as though they had crowded their way in between the coarse pieces of shell and coral" (Parker, 1908).

The Lancelet is a segmented animal, as is plainly seen in the musculature, and as can be seen in the way the nerves

come out from the spinal cord and in the way the ganglion-cells are disposed at and in their roots, and the segments show a relative independence in locomotion, which reminds us of what is seen when certain worms break into pieces. "A short piece of the tail-end can swim well and behaves much as a whole animal does; and this for many days together. To illustrate by a complex movement, normal animals in a shallow dish persistently put their heads up over the edge of the dish and then by swimming round the dish and pushing against the edge succeed in wriggling over, if the edge is not too high. The isolated tail makes the same persistent and apparently purposeful efforts when the dish is nearly full of water. When an animal is so macerated that *all* the tissues except the notochord are gone from the middle of the body, the two parts perform typical swimming movements but each with an independent rhythm. This retention of the power of coöordinated movement by a few isolated segments is perhaps connected with the large number of cutaneous fibres which have a short course in the spinal cord. This makes it possible for the muscles to be reflexly controlled by stimuli received at the surface of the body in the same or adjacent segments." (J. B. Johnston, 1905, p. 124).

We owe to Professor G. H. Parker a very valuable study<sup>1</sup> of the sensory reactions of *Amphioxus*, and we propose to give a summary of the chief results. Professor Parker's general idea in his research was to discover whether Lancelets were not primitive in activities, as well as in structure and development. "As the structure of *Amphioxus* throws light on the complex organization of the Vertebrates, so its activities may give some indication of the way in which the more complex functions of these animals have come into being."

(a) *Sensitiveness to Light.*—Lancelets are very slightly sensitive to light, for although several observers have described the wild excitement when a lighted candle is taken into a dark room where the Lancelets are being kept, a more careful scrutiny has shown that when the light first falls on the dish a few move slightly and jostle others, and then in an instant the whole assembly is in wild confusion. "It would seem that,

<sup>1</sup> "The Sensory Reactions of *Amphioxus*," *Proc. Amer. Acad.*, xlvi. (1908), pp. 415-55.

while light was the initial stimulus for a few individuals, the wild and excited swimming which gave the impression of great sensitiveness to light was not due directly to this factor, but to mechanical stimulation caused by mutual contact."

Professor Parker found that Lancelets that had been kept in the dark for some time would usually respond to light of not more than a few candle-meters intensity, but that the same individuals after lengthy exposure to ordinary daylight often failed to respond to a beam of strong sunshine. This is interesting in showing that "the capacity of the animal to respond to light is more or less determined by its previous condition, its sensitiveness diminishing with continual exposure to light and increasing when the light is excluded from it". Another interesting point is that *Amphioxus* responds to a rapid *increase* of light, but not to a rapid decrease. It need hardly be said that by using a heat-screen the experimenter made sure that the light-reactions were not really reactions to radiant heat.

The next step was to discover by what structures Lancelets are sensitive to light. Is it by the whole skin, or by a conspicuous anterior pigment spot, or by a row of "eye-cups" which lie along the nerve-cord? Professor Parker devised an arrangement for bringing a beam of light to bear on any desired part of the animal's body. Experiment soon showed that the anterior pigment spot is not merely unimportant—but insensitive—a result confirming what previous experimenters had noticed, that the removal of the whole anterior tip made no difference to the light-reactions. The exact portion of the Lancelet that is stimulated by light corresponds to that in which the nerve-tube contains the small "eye-cups" described by Hesse. "This correspondence is so precise that it seems very probable that these organs are the true photo-receptors." The skin may have something to do with it, but the distribution of the sensitiveness in different species corresponds to the distribution of the "eye-cups".

*Amphioxus* swims away from light and comes to rest in darkened situations. It cannot "see" in the sense of forming an image, and "the light about it has little or no influence except when it falls with full intensity on the animal's body". This is to be connected with the fact that *Amphioxus* is essentially a burrowing animal. Several observers have noted

that *Amphioxus* remains buried in the sand during the day (except perhaps for its anterior end), but that it leads a more active life at night. Parker's observations on *Branchiostoma caribbaeum* showed no evidence of nocturnal activities.

(b) *Sensitiveness to the temperature of the water.*—Professor Parker has shown that heat has at least two influences on Lancelets. It stimulates them to momentarily vigorous locomotion, and, in excess, it brings about death by coagulation, which begins at about 40° C. They swim away from any source of considerable heat just as they do from bright sunshine, so that, if we say the same thing in technical words, they are negatively thermotropic and negatively phototropic. They are stimulated to active swimming by water colder than 31° C., and they are killed by prolonged exposure to water of 4° C., or lower. "That *Amphioxus* should be stimulated by cold, but not influenced in a directive way by this stimulus as it is by heat, favours the view that it possesses, like some higher vertebrates, separate receptors for heat and for cold."

*Amphioxus* is very sensitive to mechanical stimulus, the most sensitive parts being the oral hood and the buccal cirri. It will also respond to sound-waves. Professor Parker says: "If a glass vessel that contains resting *Amphioxus* partly buried in the sand is gently tapped on the side, the animals, as Rice observed long ago, usually withdraw temporarily below the sand, or at least move their cirri in a way that resembles winking. That this is not due to the vibration of particles of sand against their bodies is seen from the fact that at least the reaction of the cirri can be called forth from animals that are resting on a bed of cotton wool in a glass vessel of sea-water when the walls of the vessel are tapped. . . . It is very probable that these reactions to sound depend upon the stimulation of some part of the tactile mechanism, for in the first place *Amphioxus* has no special organ that can serve it as an ear, and secondly, many sound-vibrations can be sensed through our tactile organs as well as our ears."

*Amphioxus* rests quietly when its body is in contact with particles. These are normally sand particles, but particles of glass will serve! This curious experiment corroborates what is otherwise clear, that the Lancelets do not enter the sand to escape the light.

The whole outer surface of the Lancelet's body is sensitive to chemical reagents of varied kinds, such as nitric acid, alcohol, turpentine. "This sense," Professor Parker says, "is doubtless serviceable chiefly as a means towards escape from unfavourable chemical surroundings and probably has little or nothing to do with the direct feeding habits of the animal. As is well-known, *Amphioxus* does not seek its food, but takes what is brought to it in water currents, selecting from this supply only in the crudest fashion, if in fact it can be said to select at all." It is probable that the undifferentiated chemical sense-organs or sense-cells in the skin of the Lancelet represent a state of affairs antecedent to the specialisation of the senses of taste and smell, although it is possible that a minute pit at the very front end deserves the name "olfactory" which it usually gets. Similarly, it is probable that the tactile sense-organs or sense-cells in the skin of *Amphioxus* represent the elements from which the lateral-line organs of fishes and the ears of Vertebrates in general have been derived. On embryological grounds it is likely that specialised tactile organs gave rise to lateral-line organs, and that from certain of these lateral-line organs the ear was differentiated. "This history, based upon morphological considerations, is parallel to what is known of the physiology of these parts, for the lateral-line organs are stimulated by material vibrations of low rate, possibly also effective as tactile stimuli, and the ear is stimulated by material vibrations of a higher rate, such as we recognise as sound. In my opinion, Prof. Parker continues, the stimuli for these three sets of sense-organs may often overlap and the three sets of organs constitute a genetic series, in which the tactile organs are the oldest members and the ear the newest."

"*Amphioxus* may, therefore, be said to be an animal that possesses *in potentia* at least the sense-organs of the vertebrates. Its outer surface is provided with tactile organs, but it does not possess the derivatives of these, the lateral-line organs and the ear. Its outer surface also contains undifferentiated chemical sense-organs, but it cannot be said to have a sense of taste, and the only evidence of a sense of smell is morphological. Its outer surface, like that of the higher vertebrates, contains temperature organs. *Amphioxus* also has

in the walls of its nerve-tube photo-receptors, which may well be the forerunners of the rod and cone-cells of the vertebrate retina. It is thus an animal of fundamental importance for the understanding of the vertebrate sense-organs" (Parker).

### DEVELOPMENT AND LIFE-HISTORY

*Development.*—The sexes are hardly distinguishable. There are twenty-six pairs of simple sacs—ovaries or testes—projecting into the atrial cavity. The eggs of *Amphioxus* are transparent spheres about  $\frac{1}{250}$  in. in diameter. They pass out of the atriorepore and are fertilised in the water. The segmentation is complete and almost equal. As if cut by an invisible knife, the egg divides vertically into two cells. Another vertical cut, at right angles to the first, leads to the four-cell stage. The next cut is in a horizontal plane equatorially, at right angles to the two others; and thus eight cells are formed. But the four cells in the lower part of the egg are larger than the upper four. As division goes on, a hollow ball of cells is formed, a blastula or blastosphere, and by a process of unequal growth one hemisphere is indimpled or invaginated into the other, as one might indimple a punctured india-rubber ball. Thus there is formed a two-layered embryonic stage, known as the gastrula—of very wide occurrence among animals. The outer layer is called ectoderm or epiblast; the inner layer endoderm or hypoblast, and the cavity is called the primitive gut or archenteron.

The gastrula elongates and its aperture (the blastopore) becomes narrower. A flattening occurs along the dorsal median line, the ectodermic part of which is the foundation of the nerve-cord, while the endodermic part is the beginning of the skeletal notochord. The ectodermic plate becomes a groove (the neural or medullary groove) which is over-arched in a quite unusual way by a growth of the lateral ectoderm. Somewhat later the neural groove closes in of itself to form a neural canal, which opens posteriorly (*via* the blastopore) into the gastrula cavity, and anteriorly to the exterior by a minute hole (the neuropore).

The cavity of the gastrula becomes the gut: along its roof the foundation of the notochord is seen at a very early stage; and pouches grow out which form the middle embryonic layer or mesoderm and the primary cavities of the body.

As is common when there is very little yolk, the develop-

ment of the Lancelet is rapid. In a few hours after fertilisation the gastrula may be seen rotating within the still unbroken egg-envelope; in eight hours it is hatched or set free; it swims about for twenty-four hours or so while its essential organs are being laid down; about the thirty-sixth hour it gets an open mouth and anus and a gill-cleft, and we call it a larva.

The young larva (Plate XXXIV., C) has a ciliated ectoderm, like a young tadpole and is more active than later stages. One of its peculiar features is the lack of symmetry—the mouth is to the left side, the gill-slits are to the right, the anus is median. Later on this asymmetry is considerably lessened, but there are many expressions of it in the full-grown animal.



# SECTION VI

## TUNICATES

### CHAPTER I

#### STRUCTURE

General characters ; a typical solitary Tunicate.

THE animals generally known as Tunicates or Ascidiants, more technically called Urochorda, occupy a remarkable position in the animal kingdom. As adults, few of them show any likeness to any other animal type, and the affinities which a deeper knowledge reveals are in an unexpected quarter. Their relationships turn out to be with vertebrates or backboned animals. But though the vertebrate characteristics are indisputable, they are hardly recognisable except in the larval stages, and in a few forms (Larvacea) which retain their larval characters throughout life. In most cases it must be said that the larva is an organism of higher degree than the adult, for the promise of youth is generally unfulfilled. To begin with, then, let us think of the Tunicates as a set of animals that stumble at the threshold of vertebrate life. They begin well, but few of them keep it up. As it is put technically they usually undergo "retrogressive metamorphosis".

Tunicates are found in all seas and at all depths; most of them are fixed forms, living as single individuals or in compound masses formed by budding; a few of them are adapted for open sea (pelagic) life, and here again there are solitary and compound forms. It is very interesting to find an animal so high in the scale of being still experimenting with the process of repeated budding, like plants or corals, a process which is only compatible with the sessile, or passively floating condition.

A fine account of a typical solitary Tunicate will be found

in Professor Herdman's Memoir on Ascidia ("Liverpool Marine Biology Committee Memoirs," No. I., 1899). We do not propose to do more than give a general picture of the structure, enough to serve as a basis for some remarks on the natural history of these animals.

A common shape is like a double-necked leather bottle (Plate XXXIV., D) and it is to this that the word Ascidian refers. At the upper end there is an inhalant opening or mouth; somewhat to the side there is an exhalant aperture. When the Ascidian is touched, it can send a jet of water from either opening, hence another name, "sea-squirt". The name Tunicate refers to the clear "test" or "tunic" which surrounds the animal and fixes it to rock or sea-weed. This "test" begins as a structureless cuticle,—a non-living layer secreted by the underlying living skin, and it has the peculiar interest of consisting mainly of cellulose, which is a very characteristic vegetable substance, forming the cell-walls in plants. In a very passive part of a very sluggish animal we find a characteristic vegetable substance. As the animal grows a little older, migrant cells (from the middle embryonic layer or mesoderm) wander into the cellulose test, and some cells of the epidermis seem also to pass in, so that what began as a cuticle ends with being a sort of tissue, including pigment cells, bladder-like cells, and outgrowths of the body-wall with blood-channels.

When the test is cut away, the body-wall of the Ascidian is seen, and there are two points of special interest. It is traversed by long spindle-shaped *unstriped* muscle-fibres—the kind of muscle-fibre that is found in sluggish animals or in the slowly-moving internal parts of active animals, such as the wall of the food-canal and the bladder. Between the two openings, lying on the margin, there is an elongated nerve-ganglion, the remains of the anterior part of the dorsal nerve-cord which is present in the larva.

This ganglion defines the dorsal median line, and if we now hold the animal in a position similar to that of our own body, we see that it is the right-hand side of the animal that is so abundantly traversed by the muscle-fibres, while the left-hand side is quite different, showing a twisted intestine and reproductive organs.

If we pin down the Ascidian on a dissecting block under water, and cut up the middle of the right side we expose a large cavity with a beautiful basket-work wall with innumerable minute ciliated meshes. The cavity is the pharynx and the meshes are the (secondary) gill-slits. (Plate XXXIV., E.) Water is continually passing in by the mouth, through the basket-work, and out by the exhalant aperture. The details of this are not easy, and we shall simply mention that between the body-wall and perforated pharynx-wall there is a cavity called peribranchial or atrial which communicates with the exhalant aperture. As the water passes through the slits in the pharynx it parts with oxygen to the blood-vessels (spread out between the slits) and gains carbon dioxide. The chief use of the pharynx is thus respiratory.

The food supply consists of microscopic plants and animals which are swept in along with the water. They would be swept out again through the slits were it not for an interesting contrivance. They become entangled in a "spider's web" of viscid mucus which collects at the front end of the pharynx or branchial sac. This mucus is made by a gutter (called the endostyle) which runs along the ventral margin of the pharynx—a gutter which has its precise counterpart in a groove along the floor of the pharynx in the Lancelet, and, according to some authorities, in the thyroid gland of higher Vertebrates. The entangled food particles form thread-like ropes which are wafted along the dorsal wall of the pharynx where there is a ciliated ridge or a row of ciliated tags. The ropes of food-particles are led to the opening of the digestive portion of the gut, thus passing to the left-hand side.

We rightly regard the sea-squirt as a sluggish animal, but we must not forget that here, just as in a sponge, there is great internal activity, namely that of the microscopic lashes or cilia. "All the stigmata (of which there may be several hundred thousand) in the wall of the branchial sac are bounded by cubical or columnar epithelial cells, which are ciliated. These cilia, so long as the animal is alive, are in constant motion, so as to drive the water onwards, and it is this constant ciliary action in the walls of the branchial sac that gives rise to the all-important current of water streaming through the body" (Herdman).

We have spoken so far of the mouth and the respiratory pharynx, the rest of the food-canal—the digestive and absorptive region—lies like a distorted S on the left-hand side. It is possible to distinguish a gullet, a stomach, and an intestine; and there is often a definite gland opening into the stomach. Along the whole length of the intestine there is an inturned pad (the typhlosole) which helps to increase the digestive absorptive surface. A similar arrangement is found in the earthworm. Covering the walls of the intestine to a greater or less extent are curious clear vesicles without openings which contain uric acid and are without doubt of the nature of kidneys. The nitrogenous waste-products are filtered out of the blood, but they are not directly eliminated from the body. This is a fact of peculiar interest; it suggests a constitutional defect that may have something to do with the sluggishness. We may recall the fact that plants do not get rid of their nitrogenous waste-products, but accumulate them within the body (sometimes in the form of crystals or of pigment). We may note also the retention of nitrogenous waste in many winter-sleepers, and the fact that coma sometimes supervenes in man when the kidneys cease to filter out the poisonous nitrogenous waste. It may be that the Tunicates suffer from auto-intoxication with uric acid. To some extent, however, helped by bacteria in the vesicles, the waste may diffuse out.

We have seen that all that remains of the larval spinal cord and brain is a single elongated ganglion between the two apertures. It gives off nerves at both ends to the lobes of the apertures and the muscles which close them. On its ventral surface there is a small "sub-neural gland" of unknown function, which has a duct running forwards and opening into the front of the pharynx at a sensory projection called the dorsal tubercle. It is maintained by some authorities that the sub-neural gland corresponds to the pituitary body of higher animals (a minute downgrowth from the floor of the brain meeting a minute upgrowth from the roof of the mouth). The adult sea-squirt has neither eye nor "ear," though its larva has both. There is, however, considerable sensory development about the beginning of the pharynx, e.g., in the circlet of delicate inturned tentacles

It is one of the contrasts between Invertebrates and Vertebrates that the heart lies dorsally in the former and ventrally

in the latter. So in the sea-squirt one of the Vertebrate or Chordate features is the ventral position of the heart. In *Ascidia* it lies on the ventral and posterior edge of the stomach, projecting into a space (called the pericardium) which is part of the original body-cavity. It is the simplest of all hearts—a spindle-shaped contractile tube (with the only striped muscle in the body)—and it has the remarkable peculiarity that it drives the blood out first at one end and then at the other. There is at brief intervals a reversal of the circulation. We cannot go into the details of this, but we venture to quote from one of the greatest authorities on Tunicates a description of the striking phenomenon of "reversal". Professor Herdman writes: "If a small or young *Ascidia* be placed alive, left side uppermost, in a watch-glass or small trough of sea water, and examined with a low power of the microscope, the heart will be readily seen near the posterior end of the transparent body. It will be noticed that the 'beating' looks like successive waves of blood pressed through the tubular heart from one end to the other by its contractions. After watching the waves passing, let us say, from the right-hand end of the heart to the left for about a minute and a half (perhaps 60 or 80 to 100 beats), it will be seen that they gradually become slower and then stop altogether. But after seven or eight seconds a faint wave of contraction will start from the *left* end of the heart and pass over it to the right; and this will be followed by larger ones for a minute and a half, and then again a pause will occur and the direction change." It is supposed that the heart works too energetically for the circulation; the blood cannot get quickly enough through the fine channels in the branchial sac and viscera and back pressure results. It need hardly be said that there are no valves. The blood usually appears colourless except under the microscope when it is seen to contain various coloured corpuscles as well as uncoloured.

We close our brief description of a common sea-squirt with a reference to the reproductive organs or gonads. The Ascidian has both an ovary and a testis; in other words, it shows hermaphroditism. The gonads lie in the loop of the food-canal, on the left side of the body, and the testes spread over the surface of the ovary. There is an oviduct for the passage of the ova to the peribranchial cavity and thus to the exterior, and running

beside the oviduct there is a vas deferens for liberating the spermatozoa developed in the testis. In some Ascidians, such as *Ascidia mentula*, the eggs are fertilised by the sperms from the same animals, but in many cases the two sets of reproductive organs are not ripe at the same time (dichogamy) so that self-fertilisation is prevented. In some the ovary ripens first (protogynous dichogamy); in others the testis ripens first (protandrous dichogamy).

## CHAPTER II

### CLASSIFICATION AND DEVELOPMENT

Classification of Tunicates. Order I. Appendicularians. Order II. Ascidians. Order III. Salpians. Numbers, relationships. Life-history of a typical Ascidian.

THE Class Tunicata is divided into three orders: the Appendicularians, the Ascidians, and the Salpians.

#### ORDER I. LARVACEA OR APPENDICULARIANS

These are, with one or two exceptions, pelagic forms, usually of small size (about 5 mm. in length), swimming actively by means of a relatively large tail which is supported by the notochord. (Plate XXXV., A.) They retain throughout life what the Ascidians lose at metamorphosis—a long dorsal nerve-cord, a notochord, and primary gill-slits (one pair). The food-canal ends ventrally; there is no peribranchial cavity. They are able to form very rapidly a cuticular test or “house” many times larger than the body, which is from time to time thrown off and replaced.

Like many pelagic animals, they are usually transparent but some have brightly coloured spots, such as the reproductive organs; they have a very wide representation—in all seas, and some particular forms have a great range of distribution; and they often occur in great swarms, forming especially in summer an important constituent in the surface “plankton,” or floating life.

About forty species of Larvacea are known, distributed in about ten genera, e.g., *Appendicularia*, *Oikopleura* (British), *Fritillaria* (British), *Kowalevskia*, and *Megalocercus*. The genus *Kowalevskia* is somewhat apart from the others, e.g., in the absence of heart and endostyle. The largest known Appendicularian is *Megalocercus abyssorum* from deep water in

the Mediterranean, which attains a length of 3 centimetres and has a bright red colour that is not uncommon in abyssal animals.

The "house" of Appendicularians is a very interesting structure, illustrative of the multiple utility that is often found justifying the existence of what seem at first sight like exuberances. It is a gelatinous non-living cuticular investment, made by tracts of large ectoderm cells, and quite transient. Lohmann has shown that it has some hydrostatic value, that it is protective since the tenant can escape its enemies by flitting from its house, and thirdly that it serves with its complicated passages and pores as a great sieve for microscopic food-particles.

There are two views as to the position of Larvacea. Accordingly to some they represent the primitive type, and the sedentary Ascidians are more remote. According to others, e.g., Perrier, the sedentary simple Ascidians, e.g., Julin's Mediterranean *Archiascidia*, are nearer the ancestral vertebrate stock, and the Appendicularians are specialised pelagic forms which remain at a larval level.

## ORDER II. ASCIDIACEA OR ASCIDIANS

In contrast to the Larvacea, the Ascidians have in adult life no trace of tail or notochord; they have a permanent test into which cells migrate; they have a large respiratory pharynx and the primary gill-clefts open to the exterior are replaced by usually numerous secondary slits opening into a peribranchial or atrial cavity. There are three groups, the sedentary Simple Ascidians, the sedentary Compound Ascidians, and the free-swimming colonial Pyrosomes.

The SIMPLE ASCIDIANS are usually solitary, but they are linked to the Compound Ascidians by the family Clavelinidæ. These Clavelinids are, on the one hand, the simplest of Simple Ascidians, and, on the other hand, by forming small groups of connected individuals, they reach on to the Compound Ascidians. A single individual buds off others, and these bud off others, till a small "gemmarium" is formed, in which each member has a distinct test, and is complete in itself, yet all share the same blood-system, and are connected by (epicardiac)

tubes which unite the branchial sac of one individual to that of its neighbours.

Among the five hundred or more Simple Ascidians the following British forms may be mentioned : *Clavelina lepadiformis* and *Perophora listeri*, common Clavelinids in shallow water off the coast ; *Ciona intestinalis* and *Ascidia mentula*, two of the commonest of our Ascidians ; *Corella parallelogramma*, common in the zone of coralline Algæ, with a crystalline test through which the beating of the heart and the like can be readily seen ; *Styelopsis grossularia*, found under stones at low tide, and sometimes known as "the red-currant squirter" ; *Molgula oculata* with a test of a walnut's size covered with gravel or shell and *Engyra glutinans* of a small hazel-nut's size, almost covered with sand, both living freely on the floor of the sea at a depth of ten to thirty fathoms. I have collected many specimens of the last-named in dredging off the Arran coast.

Very interesting in a simple way is the adaptation often seen in Simple Ascidians which live in the deep sea. They are raised on relatively long stalks which bear them up beyond the risk of being smothered in the fine ooze. This adaptation may be seen in *Hypobythius calycodes* from 2900 fathoms ; in *Corynascidea*, Herdman, in *Culeolus*, Herdman, which is represented at 2425 fathoms ; in *Boltenia*, *Styela*, and other forms. At various points in the animal kingdom we find the same simple adaptation to abyssal life, the development of a stalk to lift the animals out of the mud—in sponges, like the glass-rope sponge (*Hyalonema*) ; in Alcyonarians, such as *Umbellula* ; in Antipatharians which belong to the Sea-Anemone alliance ; and in Crinoids or Sea-Lilies. It is this aspect of things which this book is intended to illustrate, and although Tunicates are not very familiar animals, nor very attractive to those who do not know them, nor exhibiting much in the way of habits, they may serve to show how the members of a rather small class are adapted to very varied modes of life—in the open sea, on the shore, and in the great abysses.

The COMPOUND ASCIDIANS form by budding compact masses in which the individual members or "ascidiozooids" are buried in a common investing substance and have no separate tests. As we have seen, they are linked to the Simple Ascidians

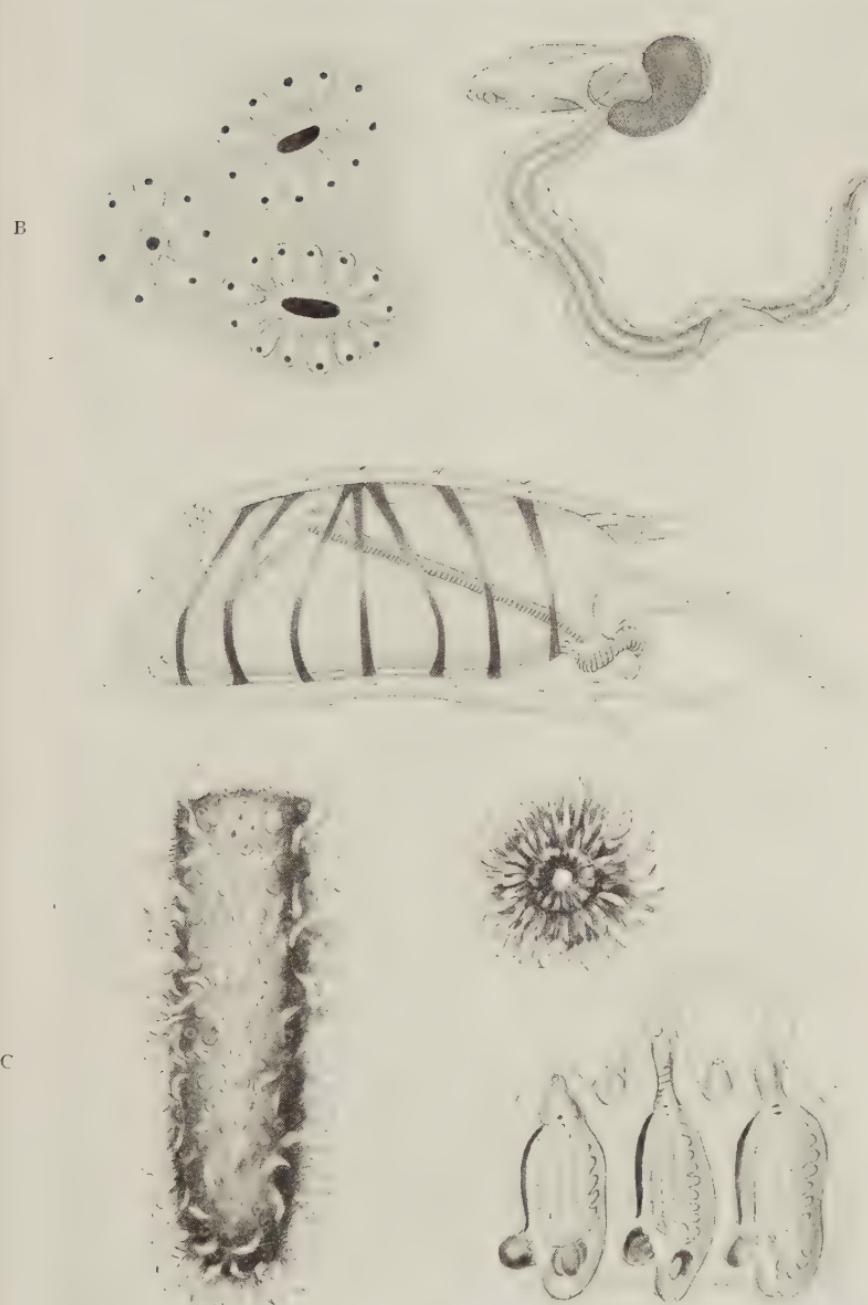
by the family Clavelinidæ, and Professor Herdman says that they probably represent "a somewhat artificial assemblage formed of those two or three groups of Ascidians which produce colonies, in which the ascidiozooids are so intimately united that they possess a common test or investing mass". Among the genera are *Distoma* (with some British species), *Leptoclinum*, a very common British genus forming crusts under stones at low tide, *Botryllus* and *Botrylloides*, as beautiful as they are common. (Plate XXXV., B.)

The free-swimming, pelagic, compound PYROSOMES or Ascidiæ Luciæ have the form of a hollow cylinder, closed at one end. "The ascidiozooids forming the colony are embedded in the common test in such a manner that the branchial apertures open on the outer surface and the atrial apertures on the inner surface next to the central cavity of the colony". (Herdman, *Cambridge Natural History*, vol. vii., 1904, p. 90.) The Pyrosomes (genus *Pyrosoma*) (Plate XXXV., C, D, E) are found near the surface, chiefly in tropical seas, and are brilliantly phosphorescent. The compound individual or "gemmarium" is often as long as one's arm, and it may be twice the length of one's body. It is said that fishermen have sometimes used yard long Pyrosomes as beacons at close quarters. At all events, on a dark night they would be better than nothing.

### ORDER III. THALIACEA OR SALPIANS

These are free-swimming pelagic forms, either simple or compound, without hint of tail or notochord in adult life, with a permanent clear test strongly or slightly developed, with more or less complete circular bands of muscle round the body, with a quite peculiar respiratory pharynx and peribranchial cavity, with alternation of generations in the life-history, sometimes complicated by polymorphism. There are two main types, Cyclomyaria, with complete circular bands of muscle around the body, e.g., *Doliolum*; and Hemimyaria, with muscular rings usually incomplete, e.g., *Salpa*.

In *Salpa* (Plate XXXV., F) a solitary asexual form buds out a stolon with prolongation of the most of the important organs of the parent. This stolon becomes segmented into a series of young "chain" individuals. Each member of the chain is sexual, and may, whether in the chain or free, produce



A.—AN APPENDICULARIAN (*FOLIA AETHIOPICA*), FROM THE SARGASSO SEA, AFTER LOHmann. THE MOUTH IS TO THE LEFT, THE DARK MASS ON THE RIGHT IS THE OVARY; THE NOTOCHORD RUNS DOWN THE MIDDLE OF THE TAIL. B.—PORTION OF A SPECIMEN OF *Batryclus*, SHOWING THREE SYSTEMS OF ZOORDS. THE CENTRAL APERTURE IN EACH SYSTEM IS THAT OF THE ATRIUM, THE SMALLER APERTURES SURROUNDING IT ARE THE MOUTHS. C.—A COMPOUND INDIVIDUAL (*GEMMARIUM*) OF PYROSOA. D.—OPEN END OF SAME. E.—THREE ZOOIDS OF SAME ENLARGED, MOUTHS ABOVE, ATRIAL APERTURE BELOW. F.—*SALPA DEMOCRATICA*, A SEXUAL INDIVIDUAL. THE MOUTH IS TO THE LEFT, ATRIAL APERTURE TO THE RIGHT; THE OBLIQUE BAND ACROSS THE CAVITY IS THE "BRANCHIA."



solitary embryos which develop into solitary Salps. This is the puzzling phenomenon of the alternation of generations—the alternate occurrence in one life-history of two or more different forms differently produced, and it is interesting to study the phenomenon where it was first discovered (by the poet Chamisso), in the Salps.

At the present time it seems legitimate to say that just as the Clavelinidæ may have linked the Ascidiæ Simplices to the Ascidiæ Compositæ, so the Thaliacea may have arisen from a stock of ancestral Compound Ascidians which gave rise to the Pyrosomes.

Compared with many others the class of Tunicates is a small one, but over a thousand species are now known. In Herdman's *Revised Classification of the Tunicata* (1891) there was a record of 538 species, and the list has been almost doubled since, mainly by the exploration of new areas. The great majority of the additions made to the roll of Tunicates since 1891 are sedentary forms.

The number of species often raises very interesting problems. There seem to be variable types which have given origin to many species, and conservative types which have few specific representatives. In the case of sedentary Tunicates a large number of species belong to a few genera or groups of genera. In this connection Professor W. E. Ritter<sup>1</sup> says: "The most conspicuous groups from this standpoint are 1, *Ascidia*; 2, *Molgula*; 3, *Cynthia* with its close ally *Rhabdocynthia*; 4, *Styela*, with the scarcely distinguishable *Polycarpa*; 5, *Botryllus* and its close congener *Botrylloides*; 6, *Amaroucium* with its near relative *Aplidium*; and 7, *Leptoclinum*. These seven groups contain more than 600 of the approximately 1000 species of simple and compound Ascidians now described. There are recognised at least 80 genera in these two Tunicate sections. In other words, as our scheme of classification now stands less than 14 per cent of the genera contain fully 60 per cent of all the species. It will be observed that these few prolific groups present all the leading types of sedentary Ascidian organisation." Ritter goes on to say, "I do not believe there is anything in our present knowledge of Ascidian structure, function, or distribution,

<sup>1</sup> "The Significant Results of a Decade's Study of the Tunicata," *Amer. Naturalist*, xli. 1907, p. 455.

to warrant the conclusion that the groups most abundant in kinds are so because of their greater fitness to survive or their relative adaptability to external conditions". The conclusion to be drawn is that the mysterious quality of varying so as to give rise to new species is strong in some types and weak in others, but this is quite apart from individual surviving power.

The Tunicates offer a fine illustration of the use of embryology in classification. Now that we know the development, we can detect certain Chordate affinities in the adult Ascidian, but it is unlikely that these would have been detected if anatomists had remained ignorant of the development. This remark does not apply to the few types of Larvacea which retain their Chordate characters throughout life. The reasons for ranking Tunicates with Chordata are to be found in the larvæ, and in the Larvacea. The five important points are:—

- (1) There is a dorsal nerve-cord with anterior expansion (or brain); (2) from this expansion a "brain-eye" arises; (3) there is an endodermic "notochord" in the region of the tail; (4) there are gill-clefts opening from the pharynx to the exterior; and (5) there is a ventral heart.

The progress of research since the days of Kowalevsky has not weakened the confidence of zoologists in the Chordate nature of Tunicates, but some of the homologies which were suggested have not been confirmed. Thus, it is very doubtful (Seeliger, Metcalf) whether the downgrowth from the brain of the Tunicate is homologous with the Vertebrate hypophysis, and very doubtful (Seeliger) whether the ventral groove or endostyle in the Tunicate pharynx is comparable to the thyroid gland of Vertebrates.

The absence of segments in the larval Tunicate is surprising in a type which has so many indubitable Chordate affinities. There seemed for a time that there were definite traces of metamerism in the tail of *Oikopleura* (one of the Larvacea), but this has not been borne out by subsequent work.

The tests of Tunicates afford attachment to numerous animals, such as hydroids, tubicolous polychaëts, acorn-shells, polyzoa, and the bivalves *Anomia ephippium* and *Modiolaria marmorata*. Dozens of the latter are often found deeply embedded in the tests of *Ascidia mentula*.

In this book different kinds of animals are used to illustrate different biological ideas, and as the Ascidians have not, for instance, much in the way of habits, we use them to illustrate, *inter alia*, the turns and twists of life-history. Everyone is familiar with the contrast between caterpillar and butterfly, or between tadpole and frog, but a much more striking contrast is that between the larval Ascidian—free-swimming and energetic—and the sedentary, sluggish, somewhat nondescript adult. Let us briefly discuss the extraordinary life-history.

The egg of an Ascidian is usually a microscopic transparent sphere with little or no yolk. It is interesting to find that in some cases there are relatively large eggs with a considerable quantity of yolk, which develop within the body—usually until the tailed larvae are hatched. Here, as in many other cases, there are “oviparous” and “viviparous” types—a distinction which really means that the eggs of the former are hatched outside of the body and those of the latter inside. But the great majority of Tunicates are oviparous.

In the majority there is probably cross-fertilisation; in *Ascidia* there is often self-fertilisation; in *Ciona*, though ova and spermatozoa are ripe at once, self-fertilisation is rare.

The fertilised ovum divides and redivides, and a hollow ball of cells (a *blastula*) is formed. The ball of cells becomes indimpled, so that a two-layered sac of cells (a *gastrula*) results. This becomes elongated, like a barrel, with the cavity (the primitive gut or archenteron) and an opening (the blastopore) posteriorly. Around the posterior opening, and extending forwards along the dorsal surface, the central nervous system appears as a neural plate, which becomes a neural groove, which becomes a neural canal. In the same median plane, but at a lower level, a rod of cells is separated off, along the dorsal wall of the primitive gut, which becomes the supporting axis or “notochord” of the posterior region. The development therefore in essential features is similar to that of *Amphioxus* or a vertebrate, but we must not go further into detail—an explanation of the development of a Tunicate is to be found in most of the text-books. Suffice it to say here, that two or three days after fertilisation the Ascidian larva is hatched—like a Vertebrate reduced to the bare essentials. It lives for a short time, swimming freely in the open sea, like a minute transparent

tadpole; and then, if it is a typical Ascidian, it settles down and undergoes "retrograde metamorphosis".

Let us form a picture of the larval or "tadpole" Ascidian (Plate XXXVI., A). It has a minute oval anterior region, and a delicate vibratory tail by which it swims. Running along the axis of the tail there is a soft rod—the notochord—by the side of which there are strong muscle-bands. Above this, along the dorsal median line, just below the surface, there is the tubular nervous system, that expands anteriorly into a "brain" or cerebral vesicle. In connection with the roof of the latter there is an unpaired "brain-eye"—an intra-cerebral eye, that does not get out of the vesicle. On the floor there is an otolith. An intucking of the outer embryonic layer (the ectoderm) forms the mouth, and in a very complex manner—far beyond our present level of description—two or more gill-slits are formed, opening from the pharynx through the atrial cavity to the exterior. Of the essential chordate characters, the larval Ascidian has five: (1) a dorsal tubular nervous system (very delicate posteriorly), (2) a supporting rod or notochord (confined to the tail-region), (3) gill-clefts, (4) a ventral heart, (5) a brain-eye. There is no definite segmentation of the body, and there is no trace of nephridia.

But the definitely Chordate larva is the creature of a day. It swims about for a few hours, perhaps for a day, and then it attaches itself to some stone or seaweed by one or more of three glandular papillæ borne on the front of the head below the mouth. (Plate XXXVI., B.)

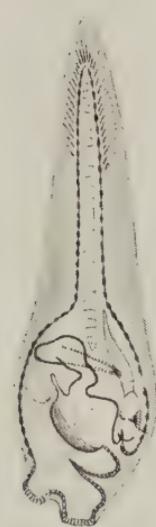
With great rapidity degeneration sets in. The tail—with its notochord, nerve-tube, and muscles—is absorbed (and to a slight extent lost in shreds). Wandering amœboid cells or phagocytes, which are present in all animals except Thread-worms and Lancelets, help in the absorption of the tail, and migrate into the anterior body. A test grows rapidly, and replaces the attaching papillæ. By a remarkable inequality of growth the posterior part of the body is made to rotate through about  $180^{\circ}$ , so that the anus and exhalant aperture are shunted to the free extremity. (Plate XXXVI., C.) Thus in a few hours an unmistakable Chordate becomes an enigmatical nondescript.

The Tunicate's life-history illustrates rapidity of develop-

A

B

C



D



A, B, C.—THREE STAGES IN THE METAMORPHOSIS OF A SIMPLE ASCIDIAN. IN A AND B THE MOUTH LIES ABOVE THE ORGAN OF ATTACHMENT ON THE RIGHT, AND THE BRAIN IS BETWEEN THE MOUTH AND THE ATRIAL OPENING. IN B THE POSITIONS ARE SIMILAR, BUT THE TAIL IS DEGENERATING. IN C THE MOUTH HAS SHIFTED TO THE FREE END, AND THE ATRIAL OPENING TO THE LEFT SIDE OF THE FIGURE. D.—*BALANAGLASSUS KOWALEVSKII* AFTER SPENGEL, THE ANTERIOR END WITH PROBOSCIS ON THE RIGHT. E.—*CEPHALODISEUS DODECALOPHUS*, VENTRAL VIEW, AFTER M'INTOSH. F.—DIAGRAMMATIC MEDIAN SECTION OF SAME SHOWING PORTION OF BUCCAL SHIELD ABOVE THE MOUTH, AND COURSE OF THE INTESTINE



ment. In *Ciona*, for instance, the eggs are liberated at dawn and the larvæ are hatched the following night. They swim about for one or two days and then undergo metamorphosis.

Such a life-history illustrates several points very clearly. (1) No anatomist, however skilful, could have discovered from the adult Ascidian its Chordate affinities. The embryologist sometimes gives a clue to the classifier. (2) In a very general way it may be said that individual development (or ontogeny) tends to recapitulate the main steps of racial evolution (or phylogeny). In most animals this is particularly true when we consider the stages in "organogenesis"; in other words, in the up-building of an organ there is a marked tendency to pass through a succession of stages which are permanently represented in a series of less highly evolved animals, representative at least of ancestral forms. To speak of an animal "climbing up its own genealogical tree" is to use somewhat rough popular language, but it is pardonable perhaps because of its vividness. But we cannot consider the life-history of a typical Ascidian without feeling that the individual development tells in a condensed form the story of the origin of these strange sluggish creatures from simple primitive Chordates.

In this connection, however, it is necessary to remember that larvæ have often characters adaptive to their peculiar modes of life; and we must not be in a hurry to reconstruct the ancestral Chordate from the young stages of forms which have certainly diverged far from the main track of vertebrate evolution. (3) The life-history illustrates individual degeneration or "retrogressive metamorphosis". "The larva," Professor Herdman writes, "is comparable with a larval fish or a young tadpole, and is thus a Chordate animal showing evident relationship to the Vertebrata; while the adult is in its structure non-Chordate, and is *on a level* with some of the worms, or with the lower Mollusca, in its organization, although of an entirely different type." Of course this is true, and yet is there not a risk of exaggerating the degeneration. The larva is of a higher type, it is a Chordate larva; the adult Ascidian is of a lower type, for it loses all the essential Chordate characteristics except the ventral heart, the gill-slits being too much modified and disguised to count. At the same time, one must not think of an Ascidian as degenerate in the sense of being undifferenti-

ated or simple. It is a very intricate animal—a very complex piece of vital machinery—which has specialised on a style of its own, departing from that of its remote ancestors, to which it returns for a brief space in its early youth. (4) One would give much to understand the deep physiological significance of the abandonment of the free-swimming habit. Do they overdo it in their youth—these energetic tadpoles; has the absence of kidney-tubes anything to do with the cessation of energetic activity; or is there some deeper vice in the constitution of which the secretion of the cellulose test gives a possible hint? *We do not know.* It may, however, be at least suggested that the whole history is the consequence of the sessile habit. Any small aquatic animal may attach itself temporarily to solid objects. The Amphibian tadpole does so. If it is able to obtain food without moving, it may remain attached longer, and if the sessile habit is thus encouraged and rewarded, it may become permanent. Thus the degeneration is the loss of structures adapted to active life, and the acquisition of an organisation adapted to stationary life.

## SECTION VII

# HEMICHORDA

Animals included in the group; structure and habits of Enteropneusta, their development and distribution; incipient species; structure of Cephalodiscus and Rhabdopleura.

**T**HREE is a widespread idea that the various big divisions or phyla of the animal kingdom stand apart from one another with sharply-defined boundaries. This is rarely the case, and it is certainly not true as regards Vertebrate or (more widely) Chordate animals. Although the actual pedigree of Vertebrates remains quite uncertain there is no doubt that the Vertebrate phylum is approached by a number of different types. Some of these are included under the title Hemichorda, a somewhat question-begging title that suggests a position on the border-line of the Chordata.

(1) Among these Hemichorda, those with clearest Chordate affinities are included in the class Enteropneusta (literally gut-breathers), represented by *Balanoglossus*, *Ptychodera*, and other genera. (2) Perhaps allied to these are two peculiar types—*Rhabdopleura* and *Cephalodiscus*, which may be united in the class Pterobranchia. (3) Still more doubtfully in this alliance is an interesting animal called *Phoronis*, which almost requires a class for itself.

Enteropneusts (Plate XXXVI., D) are soft, opaque, worm-like animals, found beneath stones or burrowing in sand and mud in almost all seas, both in shallow and deep water. Uninitiated observers would call them "worms," though the discoverer of the first one (Eschscholtz in 1825) called it a Holothurian, but they are not like other "worms," except in the most general way, e.g., in shape and burrowing habits. They have no distinct segments like an earth-worm, no gills

like a lob-worm, no limbs like a sea-mouse. The body consists of a "proboscis" in front of the mouth, a firm "collar" region behind the mouth, then a region with gill-slits, and finally, a soft slightly coiled portion. But peculiar as they are in outer form, they are still more peculiar internally. It is enough in this introductory note to say that they have got remarkable gill-slits, a dorsal as well as a ventral nerve, a strange dorsal piece of skeleton in the front of the body. They vary in length from about 1 in. to over 6 in.; they are often coloured—red, brown, greenish—and they are occasionally phosphorescent; the skin is ciliated all over and is rich in unicellular glands secreting mucus which, with the addition of grains of sand, sometimes forms a tube around the body; they have a pungent odour like iodoform (possibly of protective value); underneath the skin there is a muscular body-wall, but the fibres are of the unstriped variety, which means that they are slowly contracting; thus the locomotion, which is helped by the external cilia, by the proboscis, and by the engulfing of sand by the ever open mouth, is leisurely; the food consists of the organic particles and small organisms in the sand.

A vivid picture of the occasional activity of Enteropneusts is given by Iwaji Ikeda in a paper entitled "On the Swimming Habit of a Japanese Enteropneust, *Glandiceps hacksii* Marion" (*Annotationes zoologicae Japonenses*, vi., 1908, pp. 255-257). "Very early in the morning of 3rd September, 1907, when I was out skimming with some of my students a short distant off Sesujiima (near Tomo, about 50 miles E. of Hiroshima) in the Inland Sea, a curious sort of plankton covering a considerable area attracted our notice. On examining the contents of our net, it turned out to be swarming *Balanoglossus*. A little later, when the sun was about to rise, we could perceive myriads of lively swimming specimens about our boat. We now came to realise that we had been rowing about in a big sheet of swarming Enteropneusts. More than delighted with this sight, we collected a bucketful of specimens—a task accomplished in but a minute. They measured from 3 to 15 centimetres in length (8 centimetres on an average). The belt-like zones of this plankton varied from 1 to 5 metres in width and were in some cases 2 metres in thickness. The animals were crowded in

various degrees; at the thickest spot about 50 individuals in a cubic foot of water, while at the thinnest only about 10 in the same. After nearly 100 yards row, we came across another broader sheet of swimming *Balanoglossus*. There they were so thick that we could count nearly 100 specimens in a cubic foot of water. When the sun was up, this curious plankton almost suddenly disappeared."

This circumstantial account is interesting in showing that what we are accustomed to think of as a somewhat rare type may be very abundant in certain places and at certain times. Ikeda's picture is a fine instance of the prodigal abundance of life, and he adds another graphic touch: "On coming back to shore, we found, to our great surprise, a considerable stretch of the beach (one metre in width) covered with the deep reddish-brown *Enteropneusts*".

The species of *Balanoglossus* which was here observed was *Glandiceps hacksii*, and there are some instructive points to be noticed. (1) The ventral side is much lighter than the dorsal, which we may associate with the animal's habit of creeping on the floor of the sea at a depth of 5 to 15 fathoms. (2) The posterior region of the body is much flattened and the margins function as fins in the swimming. (3) The food-canal contained no sand, but compacted masses of diatoms and infusorians (dinoflagellates). It seems then that this *Enteropneust* is not a burrower or sand-eater, like most members of the class, but a creeper and swimmer. As "the swarming has nothing to do with sexual maturity" it may be concluded that "this form comes to the surface after microplankton, which, as we know, flourishes especially in summer months, and is most abundant in calm mornings before sunrise."

The most remarkable general fact regarding the development of *Enteropneusts* is that two distinct modes occur. This is striking when we consider that the class is relatively a very small one. In the family *Balanoglossidæ* what is called *direct* development obtains, that is to say, the egg develops into an embryo which quite gradually develops into a miniature of the adult worm. In the families *Ptychoderidæ* and *Spengelidæ*, what is called *indirect* development obtains, that is to say, the egg develops into a larva which is quite unlike a miniature of the adult, and only passes on to

that line of development after a metamorphosis. This larval form, which swims freely in the sea, often in great abundance, is called a Tornaria, and it is peculiarly interesting in showing some apparent resemblance to the larvæ of Echinoderms.

There are some facts of much interest in the development of Enteropneusts. (1) They are represented in practically all seas from Greenland to New Zealand. Moreover, Professor Benham has reported finding a species off New Zealand which seems practically the same as a Japanese form. *This widespread cosmopolitan distribution is characteristic of archaic types.*

(2) Some species occur in shallow water near shore, e.g., *Ptychodera sarniensis* from the Channel Islands; most species may be called littoral; yet *Glandiceps abyssicola* was dredged from a depth of 2000 fathoms in the Atlantic Ocean. There do not seem to be marked differences of structure corresponding to the great differences in habitat, but it should be noted that the habits (of burrowing, engulfing sand, and so on) seem to be very much the same throughout.

As an instance of the evolution-principles which it is one of the aims of this book to illustrate, we may refer to a well-known Enteropneust, called *Ptychodera flava*, Eschscholtz. This is a *species*, i.e., a group of similar individuals, "breeding true," and differing from related species in characters deemed important enough to deserve a special name. Now it has been shown by Punnett (1903) that in the group of animals collectively designated *Pt. flava* there are to be found different positions of organic stability, to which it may be convenient to give "a local habitation and a name". They may be "varieties" within the species. Furthermore, the greatest authority on Enteropneusts, Professor J. W. Spengel of Giessen, finds (1903, 1904) that *Pt. flava* from Funafuti is different from *Pt. flava* from New Caledonia or from Laysan. He proposes to give these "provisional" specific names: *Ptychodera flava funafutica*, *Pt. fl. caledoniensis*, and *Pt. fl. laysanica*; and he points out that while Funafuti ( $8^{\circ} 30' S.$ ) lies between New Caledonia ( $20^{\circ} S.$ ) and Laysan ( $26^{\circ} N.$ ) *Pt. fl. funafutica* is not intermediate in structure between the other two forms. Now the interest of these "dry details" is great—they illustrate the tendency that both animals and plants have to break up into

new varieties or possible species when they become spread out in *isolated groups* without ready intercommunication. The case probably illustrates isolation as a factor in evolution.

Two very peculiar types—*Cephalodiscus* and *Rhabdopleura*—have so many characters in common that they are included by many authorities in one order—PTEROBRANCHIA.

They are minute animals living in tubes and producing numerous buds. The “proboscis” is flattened into a buccal shield; the “collar” is prolonged into two or more feathery arms; the food-canal is bent like a U so that the anus lies dorsally near the mouth.

The individual *Cephalodiscus* is 2 to 3 millimetres in length and its appearance is not at first sight suggestive of Chordate affinities. (Plate XXXVI., E, F.) In some features, however, it undeniably resembles Enteropneusts. The body may be divided into proboscis, collar, and short trunk. The proboscis, flattened into a shield, overhangs the mouth. The collar is prolonged dorsally into 4 to 6 pairs of plume-like arms each bearing very numerous filaments. The trunk is short and globular.

The four most remarkable characters are the following: (1) Two gill-slits open from the pharynx to the exterior; (2) the chief part of the nervous system lies dorsally in the collar-region; (3) a short dorsal outgrowth from the gut in the collar-region passes into the proboscis and is comparable to a notochord; (4) there is a body-cavity in the proboscis, a paired body-cavity in the collar-region, and a paired body-cavity in the trunk. Unless these have been misinterpreted they indicate Chordate affinities, and it is a remarkable result of careful anatomy and embryology, that this type, which was originally referred to the same class (Polyzoa) as the common sea-mat (*Flustra*), should turn out to be not so very far removed from the Chordate stock. Unless there were several independent evolutionary approaches to the Chordate organisation, which is not very likely, then the ancestors of *Cephalodiscus* were on the main line which has led to Man. What would one not give to know what precisely determined the divergence of the ancestors of *Cephalodiscus*, so that they ended in being almost seaweed-like aggregates instead of going on?

Although a large number of individuals of *Cephalodiscus*

occur together, there is no compound organism in the strict sense. A stalk on the ventral surface of the body of a *Cephalodiscus* produces buds, but these are separated off from the parent. Yet they remain close together within the shelter of a secreted "house" which is almost more like a firm gelatinous seaweed than the encasement of a scion of the Chordata.

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